

43. Observations on the Anatomy of the Shoe-bill (*Balæniceps rex*) and allied Birds. By P. CHALMERS MITCHELL, M.A., D.Sc., LL.D., F.R.S., Secretary of the Society.

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(Plates LXXX.–LXXXIII.* and Text-figures 119–132.)

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In the end of June, 1912, a young example of the Shoe-bill (*Balæniceps rex*) arrived at the Gardens as a gift from the Sirdar, Sir Reginald Wingate, G.C.V.O., Honorary Member of the Society. It was not quite adult, but stood between three and a half and four feet in height. It was placed in a warmed enclosure communicating with a grassy paddock containing a small pond, and it fed well, although its appetite was small, on fish, frogs and pieces of meat. It appeared to thrive through the winter, but in the end of March, 1913, it showed difficulty in breathing. It was removed to the Sanatorium and kept for a few days in a warm, moist atmosphere, but died. The *post mortem* examination showed the presence of mycosis in the lungs, although not in sufficient quantity to cause mechanical obstruction to respiration, and the interior of the larynx and bronchi was nearly free, but subsequent microscopic examination by Mr. Plimmer, F.R.S., the Society's pathologist, revealed extensive infiltration of the tissues by the mould. As Dr. Beddard, the Society's Prosecutor, was engaged on other work, I gladly took the opportunity of making some observations on the anatomy of this rare bird, and give the results here. My work was to a certain extent limited by the necessity of not injuring the skeleton, which was destined for the British Museum (Natural History). Certain portions of the viscera were sent to the Museum of the Royal College of Surgeons.

I am indebted to my colleague Mr. D. Seth-Smith, the Society's Curator of Birds, for leave to reproduce on Plate LXXX. the excellent photograph of this bird, which was an immature male.

Pterylosis.—A. D. Bartlett (1) discovered and described the powder-down patches, and Professor Giebel (21) has written a

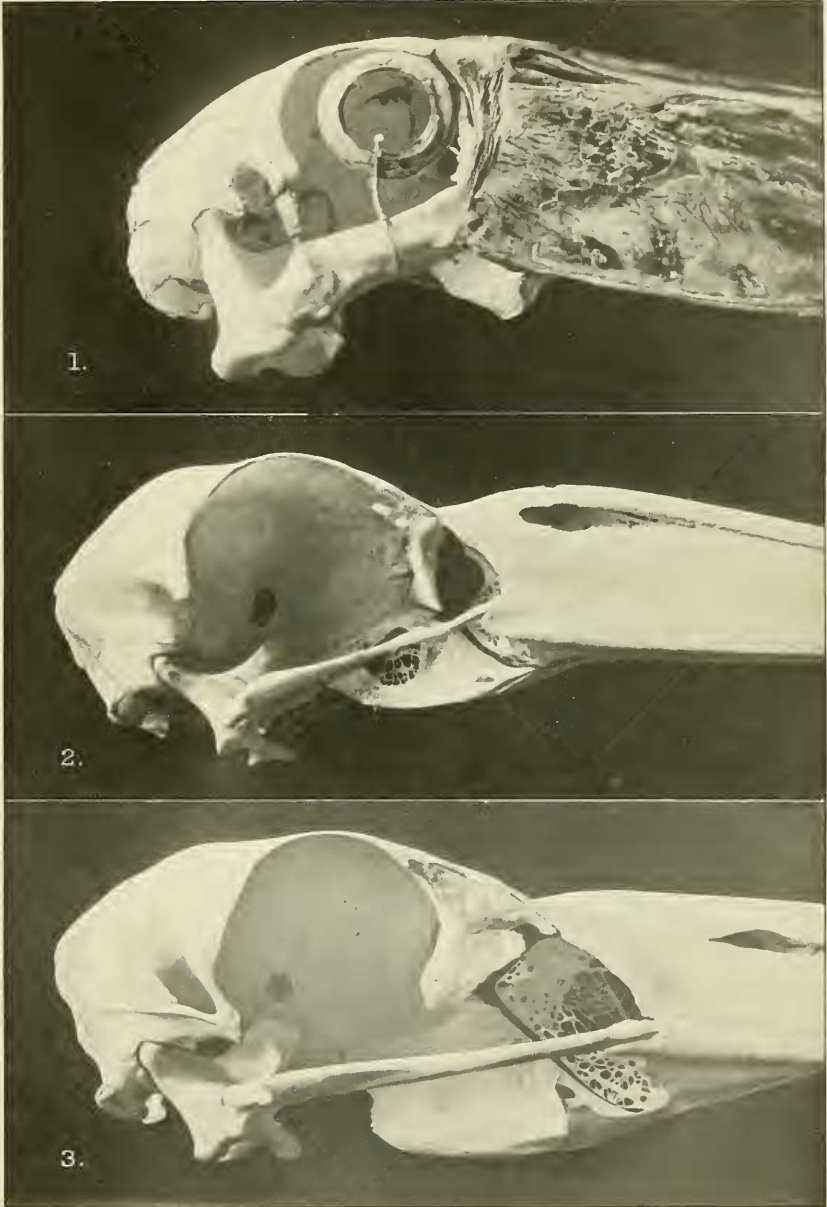
* For explanation of the Plates see p. 703.



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D. Seth-Smith, photo.

BALÆNICEPS REX.

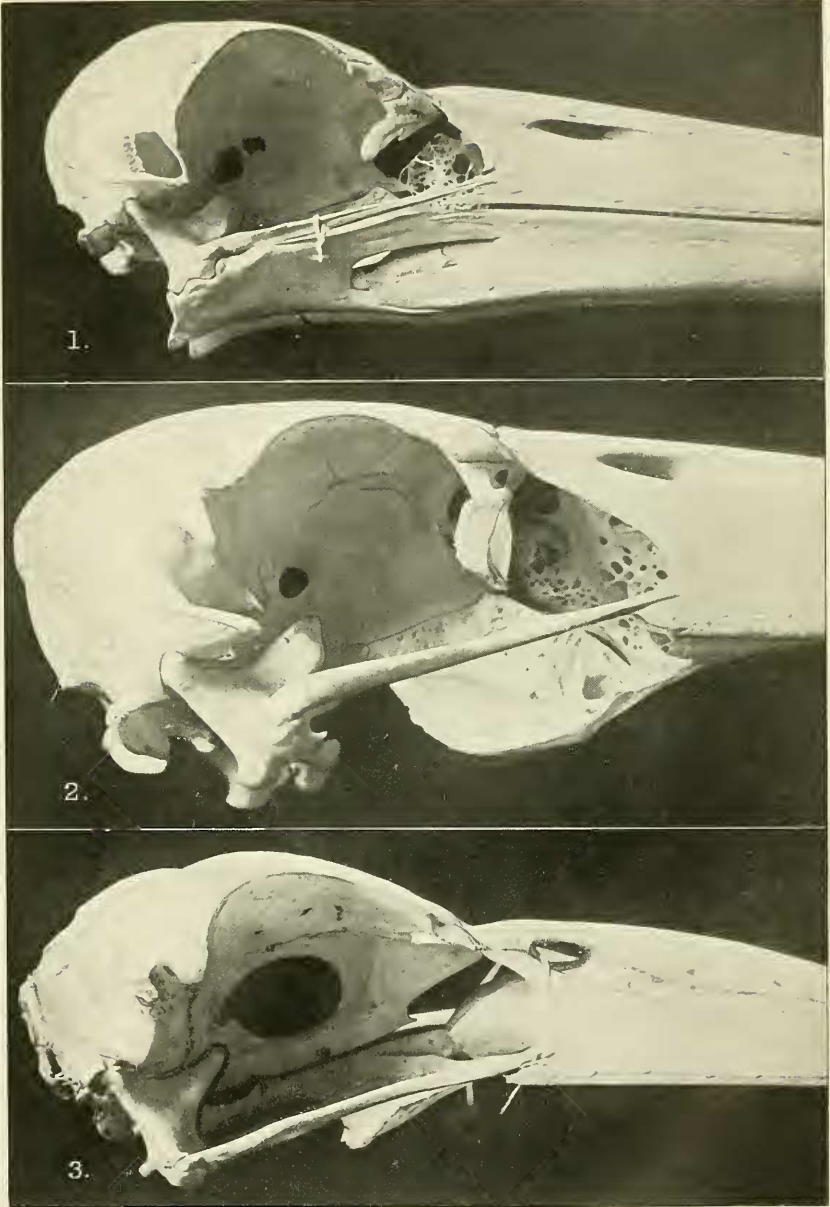


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SKULLS OF: 1. BALÆNICEPS. 2. SCOPUS. 3. XENORHYNCHUS.

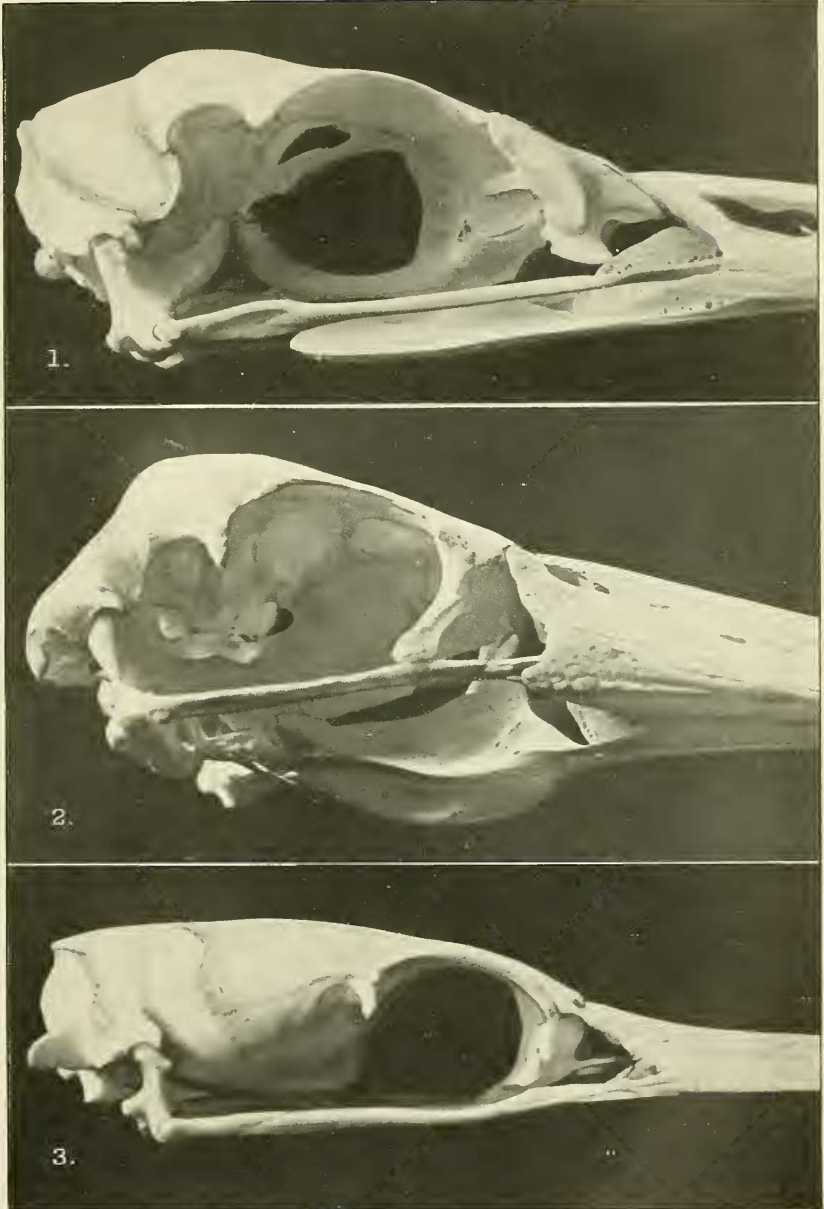




D. Seth-Smith, photo.

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SKULLS OF: 1, DISSURA. 2, TANTALUS. 3, CANCROMA.



D. Seth-Smith. photo.

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SKULLS OF: 1. ARDEA. 2. PELECANUS. 3. PLOTUS.

careful account of the external characters and pterylosis, but fortunately I finished my examination and notes of the pterylosis before having the opportunity of consulting Professor Giebel's paper, and find that my observations and inferences follow his very closely.

The down feathers are distributed practically uniformly over the pterylae and the apteria as in Steganopods and Storks, whereas in *Scopus* and Herons they are found only on the apteria. The oil-gland has a tuft of feathers as in nearly all the members of the group. The contour feathers have a small aftershaft; this structure is present in Herons and *Scopus*, variable and sometimes absent in Storks.

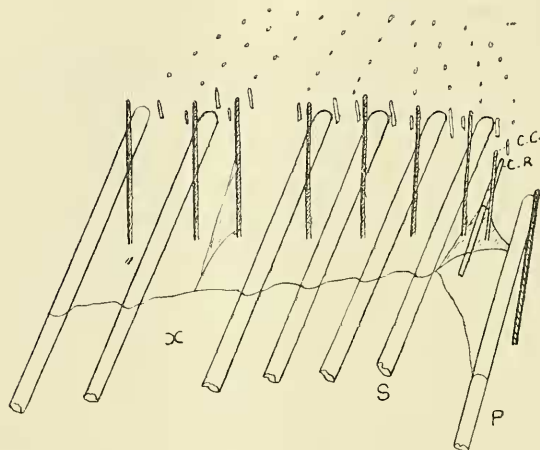
The feathered tracts generally are in marked contrast with those of Herons and resemble those of Storks in being relatively wide and fading off into the apteria, those in Herons being remarkably narrow and very sharply defined at their lateral and posterior edges. The neck is continuously feathered for almost the whole of its length, and shows no trace of the long lateral apteria characteristic of Herons and present in *Scopus*. Far back, near the base of the neck, there is a lateral space at each side. The spinal tract forks between the shoulders, leaving two parallel bands of feathers continuous with the neck area, and separated by a wide median apterion. These dorsal bands are wider than those of Herons and cease about the level of the axilla. Parallel with them at each side is a very broad and strong humeral tract, wider even than in Storks and much wider than in Herons. The dorsal tracts reappear again as a narrow diamond-shaped band, weaker in the middle line, and stretching between the powder-down patches to the oil-gland. The powder-down patch at each side is an enormous, elongated oval area extending from a little way behind the axilla to the rectrices, and reaching some way down the side of the rump. The patches are separated in the middle line. The feathers are long, very thickly set, and break down into a yellowish powder. When the bird had been in spirit, they formed unpleasant, greasy masses. Their discovery led Bartlett to associate *Baleniceps* with Herons as opposed to Storks. As, however, there are only two patches in *Baleniceps* as compared with four to six in Herons generally, eight in *Cancroma*, as they are absent in *Scopus* and exist in many other birds, e. g. *Eurypyga*, *Rhinocetus*, *Mesites*, some Tinamus, Birds of Prey, Parrots, and Goatsuckers, it is difficult to attach any systematic weight to their presence. Nitzsch's observation that they may disappear with age (e. g. *Gypaëtus*) still further destroys their systematic importance.

The femoral tracts bordering the powder-down patches are rather badly defined. The arrangement on the ventral surface is almost identical with that given by Nitzsch for *Ciconia*. The median apterion is rather indefinite except at the base of the neck and near the vent. On each side of it is a very broad feathered tract.

The rectrices are 12 in number as compared with from 8 to 12 in Herons, and 12 in *Scopus* and Storks.

The primary quills of the wing are 11, not 10 as Giebel states. Of these six are on the metacarpal, three on phalanx 1 of digit II and two on phalanx 2 of digit II, the last being much smaller than the others. There are 11 in Herons, 10 in *Scopus* and 11 or 12 in Storks. There are 19 secondaries as compared with 11 to 18 in Herons and 14 to 25 in Storks.

Text-fig. 119.



Wing-structure of *Balæniceps*.

Diagram of the distal secondary quills and coverts, showing the diastataxic condition.

Right wing; external view. The quills are in outline, the major coverts are shaded; the transverse rows are represented by dots, showing the insertion.

- | | |
|-----------------------------|--------------------|
| S. First Secondary. | C.R. Carpal remex. |
| α . Diastataxic gap. | P. First Primary. |
| C.C. Carpal covert. | |

In the figure (text-fig. 119) I give a diagram of the distal secondaries, showing the arrangement known as "aquintocubital" until W. P. Pyrcraft and I showed simultaneously (28, 36) that it was not due to the loss of a secondary feather, after which my term "diastataxic" has been used. The major coverts are inserted proximally to the quills and cross over them, and this arrangement is repeated in the case of the degenerate carpal covert and carpal remex, whereas the major coverts of the primary quills are distally placed. The diastataxic gap is very evident and the major covert, which occupies the gap, is tied down to the membrane supporting the quills by a special slip. In the same fashion the carpal remex has a membranous slip supporting it.

There is nothing peculiar in this arrangement; the diagram resembles closely the similar diagrams that I have given for other diastataxic birds (*e.g.*, 32, fig. 23). There is some difference of opinion as to whether the secondary quills, major and minor coverts, and the feathers nearer the outer border of the wing represent horizontal or transverse series. Most writers, following the obvious lead given by the quills and major coverts, have preferred to regard the rows as horizontal. I have taken the other view, seeing in the quills merely the enlarged members of the transverse rows which happen to lie along the margin of the wing and to have become the flight feathers, and the points of insertion of the feathers in the plucked wing have always appeared to me to lie in transverse or rather diagonal rows stretching upwards from the quills and reappearing on the under side of the wing in the feathers with reversed surfaces. These diagonal rows were plain in the wing of *Baleniceps*, but I was surprised to find what I have not noticed in any other bird, although I am by no means prepared to say that it does not occur, that there was a transverse row too many. The row corresponding to the carpal covert and remex curved upwards and backwards; the next most proximal row had a similar curve and belonged to the distal secondary quill; then there appeared to be an extra row in front of, and not behind the second secondary quill. More proximally the rows were in regular correspondence with the quills and gradually changed their inclination. I tried to correlate the arrangement with what W. P. Pycraft has called the "intercalary row" (a transverse row which in his opinion is associated with the mode of origin of the diastataxic gap by "faulting" of the horizontal rows in development), but was unable to make anything of it. No one appears to have published any observations on the theory of diastataxy since Pycraft and myself. In our communications to the Linnean Society (28, 36) we showed that the condition was not due to the loss of a feather, Pycraft arguing from ontogeny and I from comparative anatomy. I showed that whereas most pigeons were diastataxic, a few were eutaxic and had arrived at this condition by a secondary closing of the diastataxic gap. I also showed that the eutaxic pigeons were in other respects more specialized than their diastataxic allies. In later papers (29, 31) I showed that similar conditions existed amongst Kingfishers and amongst Gruiform birds. The general inference seems to be clear: that the eutaxic groups are more specialized birds and that in association with their general specialization they have lost the primitive diastataxic arrangement. My argument, however, may be anatomically sound with regard to the groups presenting both conditions, and yet not applicable to birds generally. All birds may have been eutaxic originally; certain families may have become diastataxic, and amongst these certain members may have secondarily reverted to the eutaxic condition. Pycraft assumes that the eutaxic condition was primitive, and if he be

correct, my facts would have to be interpreted according to the alternative I have just given. But I am not convinced by Pycraft's deduction from his observations on the ontogenetic changes in the wing. The development of the individual is partly a process of latent differences becoming visible, and because a diastataxic bird appears to be eutaxic at a very early stage, it does not follow that eutaxy was primitive. I am much more impressed by the general view that passerine birds are plainly the most specialized of all birds, that they are eutaxic, and that the members of diastataxic groups which have become eutaxic are in other respects most passerine-like. In the absence of any convincing theory of the phylogenetic origin of diastataxy, all peculiarities in the arrangement of feathers are interesting and may come to have significance, and so I have digressed with regard to the wing of *Balaeniceps*.

It is plain that the pterylosis of *Balaeniceps* is of the same general character as that in Storks, Herons and *Scopus*. To my eye, the general appearance and coloration suggest affinity with Herons rather than with Storks. The sedate habit of standing silently on any little eminence, the absence of the habit of clattering with the beak, which we noticed in the Gardens, and the reported heron-like bending of the neck in flight, confirm this view. But the actual details of the feathering do not confirm it; without any doubt, so far as pterylosis can be relied upon as indicating affinity, *Balaeniceps* is more Stork-like than Heron-like.

Petherick, however, (34) has recorded that the young ran about with extended wings making a "rattle-like noise produced by the snapping of their bills."

Foot and Claw.—The hind toe (hallux) is usually carried pointing backwards, but is freely movable in every direction. It is on the same level as the other toes, as in Herons and *Scopus*, not slightly elevated as in Storks. There is no trace of a web uniting any of the toes, whereas in Herons and *Scopus* there is usually a distinct web uniting the third and fourth toes, and in Storks all three front toes are united by web.

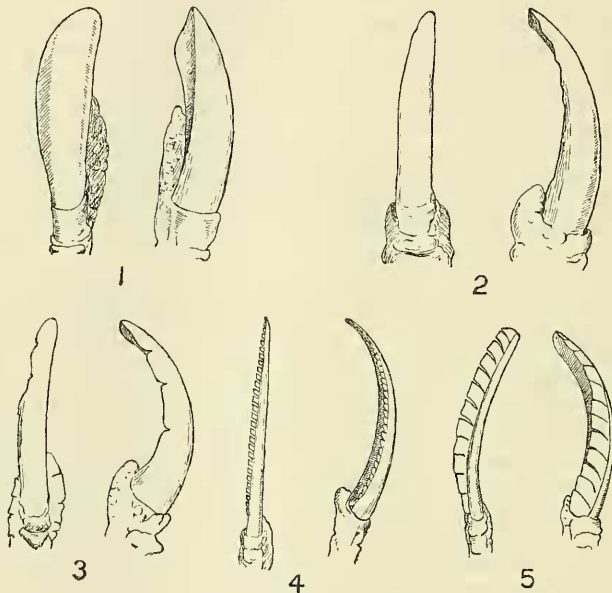
A good deal of confusion, which I am able to dispel, has crept into the literature with regard to the condition of the claw of the third digit of the foot. It is well known that the inner edge of this claw is pectinated in Herons and unbroken in Storks. Professor Reinhardt (37, p. 378) stated that *Balaeniceps* had not a comb on the middle claw, adding that this absence afforded "a strong warning not to class it with the Boatbill, as this peculiar serrature never fails in any member of the Heron tribe." Gadow (16, p. 137) divided the Ardeæ into Family 1. Ardeidæ, dividing the latter into the sub-families Ardeinæ and Balaenicipitinae, mentioning as a character of the former "Mittelkralle gezähnt," and of the latter "Mittelkralle nicht gezähnt," and Family 2. Scopidae, including in the definition of the latter, "Mittelkralle gezähnt." Beddard (3, p. 289) cites Professor Reinhardt's opinion

that "as the middle claw is not pectinated, *Balæniceps* cannot be referred to the Herons," adding "Professor Reinhardt would associate *Balæniceps* particularly with *Scopus*," but omitting to mention that in the same paper Reinhardt stated that the claw was pectinated also in *Scopus*. Mr. A. H. Evans (8, p. 87) divides the Sub-order Ardeæ into the Families Ardeidæ (in which he places *Balæniceps*) and Scopidæ, and states that in the Sub-order the "claw of the middle digit is toothed on the inner side, save in *Balæniceps*." It is surprising that as Gadow, Beddard, and Evans all seem to have thought the matter worth comment, they should have omitted to notice Giebel's (21, p. 351) very definite description. Giebel stated that in the two examples of *Balæniceps* he had examined the pectination was clear and sharp, the actual teeth being not so small, numerous and deeply incised as in *Cancroma* and *Nycticorax*, but larger, separated by wider intervals, and, beginning at the point, reaching nearly the middle of the nail. He described them as closely corresponding with those of *Scopus*, adding that the latter had not received full attention from systematists.

I hope that the drawings reproduced in the figure (text-fig. 120), which were made by Mr. Berridge from the actual specimens, will explain the matter. In a large number of birds belonging to different groups, the claw of the third toe of each foot is not symmetrical about the middle line; the ulnar or abaxial edge is relatively straight, and the radial edge, that nearest the body, is curved out into a sharp-edged scoop. The foot of the White Ibis (fig. 120, 1) shows this condition well. In *Balæniceps* (fig. 120, 2), owing to the lateral compression of the claws, the scooped edge is not quite so conspicuous in a dorsal or lateral view, but it exists. Moreover, as Giebel described, this sharp edge is marked by a few serrations between each of which there is rather a wide space, but which are so conspicuous on the claw that they can be felt not only along the edge but as slightly ribbing the surface. In *Scopus* (fig. 120, 3) the condition of the claw is almost exactly similar to that in *Balæniceps*. In the example I examined and from which the drawing was made the serrations were cut a little deeper than in *Balæniceps*, but according to Giebel, in the specimens of *Balæniceps* he examined, the serrations were deeper. The exact amount of serration is no doubt subject to individual variation. In the corresponding claw of the left foot of the Umbre I examined, each tooth was much narrower and more pointed, resembling the *Balæniceps* condition more closely. In the Little Bittern (fig. 120, 4) and in the Goatsucker (fig. 120, 5), the teeth are much more numerous, regular, smaller and more closely set together, and when the comb is highly developed, it may stand out conspicuously from the edge of the claw, sometimes by not being developed along the whole edge, and sometimes because the thin edges of the teeth give the comb a yellow semi-transparent coloration, readily visible against the duller and more opaque unbroken part. Almost every gradation

between the sharp unbroken edge and a fully formed comb can be found in nearly allied birds, and it must be a matter of individual taste at what particular stage of elaboration it is possible to describe the serration as a comb. It is at least certain that *Baleniceps* cannot be separated from *Scopus* and the Herons and associated with the Storks because of absence of pectination.

Text-fig. 120.



Modified Claw in some birds.

Claw of the third toe of the right foot, in each case the left-hand figure showing the dorsal aspect, the right-hand figure the axial side.

1. Red-billed White Ibis (*Eudocimus longirostris*).
2. Shoe-bill (*Baleniceps rex*).
3. Tufted Umbre (*Scopus umbretta*).
4. South American Little Bittern (*Butorides cyanurus*).
5. Nacunda Goatsucker (*Podargus nacunda*).

It seems obvious, however, that the formation of a comb falls in the category of what I have termed "multiradial apocentricities," modifications from the normal or primitive type, which as they have occurred repeatedly and independently, afford no information as to the systematic position of the animals in which, they occur. By the kindness of Mr. Seth-Smith I have looked through a number of the skins in the collection of the Society, and with the assistance of Mr. Ogilvie-Grant a still larger number

in the Bird Department of the British Museum. Most of the Steganopods have a scoop-like edge forming a primitive stage like that shewn in the figure (fig. 120, 1), but some of them, for instance the common Cormorant, have a well-formed comb. The small claws of Storks seem to have no trace even of the initial asymmetry, but Ibises are certainly more nearly allied to Storks than to Spoon-bills, and although the White Ibis (fig. 120, 1) has only the scoop-like edge, the Glossy Ibis (*Plegadis falcinellus*) has a well-formed comb. *Eurypyga* and *Rhinocetus* have the curved edge but no serration; *Cursorius*, *Dromas* and *Glareola* have well-marked combs. Among the Strigidae, *Scops* and some of the smaller owls have the curved cutting-edge without serration; *Ketupa* is in the same condition. *Bubo* has a well developed cutting-edge with a few slight serrations; *Strix flammea* has a well-marked comb occupying the upper part of the edge of the claw. By a curious accident of nomenclature I was led to examine some of the Birds-of-Paradise. Fürbringer mentions *Falcinellus* as a genus in which the claw is pectinated, and as I had forgotten that that name had been used for a genus of Ibis, and knew that it was used for a Bird-of-Paradise, I examined the latter, and found that the claw in the Rifle-birds usually showed a sharp cutting-edge and that occasionally (e. g. *Ptilorhis* and *Epimachus*) there were slight nicks in it.

H. R. Davies (7, p. 368) in discussing the function of this organ remarks that the "pectinated claw should not be regarded as a structure peculiar to nightjars, owls, herons, cormorants and gannets, and different from anything found in any other bird, but merely as a highly modified form of a structure found in a less modified form in many birds." There seems to be no doubt but that the chief use of the modification of the claw is for scratching, possibly for removing parasites, and its presence may be compared in a general way with the condition in the mammalian Dassies, in which all the digits are protected by flat nails, except the inner digit on each hind foot which is provided with a sharp claw used in scratching.

Rhamphotheca.—The horny covering of the beak is compound in *Baleniceps*, the premaxillary portion being separate, as in *Scopus*. In Storks and Herons it is simple. The edge of the horny lower jaw is delicately serrated.

The Syrinx.—This has been studied and figured by Beddard (3), and I have to add to his description only that the first two incomplete bronchial rings are partly calcified, that the bronchi are relatively rather long, and that the distal bronchial rings are practically complete. On the most careful examination, I could find no trace of anything corresponding to what Beddard took to be fibrous vestiges of the intrinsic muscles present in Herons; they were as completely absent as in Storks. I cannot follow Beddard, moreover, in his view that the structure of the syrinx is "conclusively in favour of regarding *Baleniceps* as a Heron and not as a Stork." So far as the syrinx of *Baleniceps*

agrees in structure with that organ in Herons and in *Scopus*, it conforms not with a structure that is specially Ardeine, but with one that is found in so many different groups that Beddard himself has spoken of it as the typical avian syrinx. Storks, as he himself has shown, display a series of stages most conveniently regarded as degenerations in different degrees from the typical avian syrinx. *Baleniceps* shows degeneration, if not complete absence of the intrinsic muscles; it has not degenerated so far as most of the Storks, but the fact is that as there is no typical ciconine and no typical ardeine syrinx, the condition in *Baleniceps* affords no clue to its relationship with either of these groups.

Carotid Arteries.—The normal condition, present in a large number of birds of different groups, and what development and comparative anatomy would seem to indicate as the primitive avian condition, is the presence of both right and left carotids, separate and well developed. This is the condition usual in Steganopods, Herons, *Scopus* and Storks. I was surprised therefore to find that only the right carotid was present in *Baleniceps*, and although I searched carefully, I could find no trace of even a degenerate left artery. I do not attach systematic importance to the condition of the carotids, as this often varies within a Family. In *Botaurus*, for instance, the two carotids fuse very close to their origin, and in another member of the Ardeidæ (*Ardetta*) the right carotid only is present.

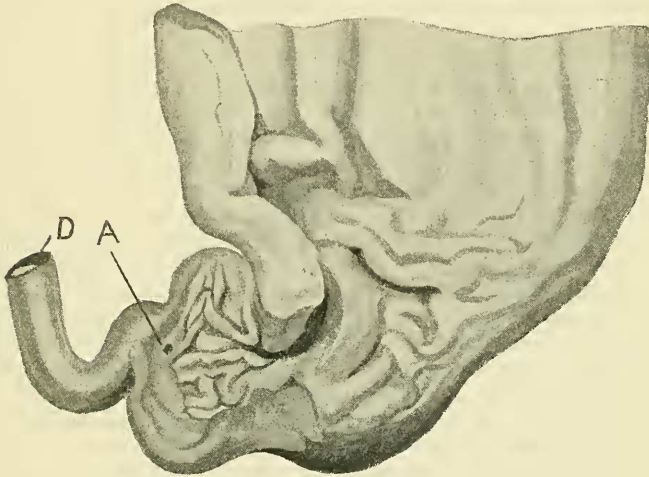
ALIMENTARY CANAL.

The tongue is only a vestige as in Storks, *Scopus* and *Cancroma*, whereas it is long in Herons.

Stomach.—The stomach is a capacious, elongated, rather thick-walled sac, extending posteriorly in the line of the œsophagus, from which it is to be distinguished externally only by a gradual increase of calibre. Distally it ends in a blunted angular point, and just proximal of this it gives off, on the right side, a globular chamber from which the duodenum arises (text-fig. 122, P, p. 657). Externally there is no trace of any specially tendinous area, and no constriction to mark off a proventriculus from a gizzard. The interior of the stomach, including the chamber at the pyloric end, is lined with a thin but well-marked layer consisting of the hardened secretion of the gastric glands. The cavity of the stomach is distinctly marked off from that of the œsophagus by the corrugated edge of the membrane-like layer of secretion. The general cavity is sharply marked off from that of the pyloric chamber by a well-marked constriction (text-fig. 121). The greater part of the interior of the larger chamber is marked by longitudinal folds, but towards the posterior end these pass into irregular corrugations which are continued into the pyloric cavity. When the internal surface is scraped and the wall squeezed, the large glandular apertures may be seen to be distributed over the whole area of the stomach and pyloric cavity,

with a slight tendency to be arranged in longitudinal bands, but there is no indication of separation into a glandular proventriculus and a muscular gizzard, and no trace of aggregation into specialized patches or areas.

Text-fig. 121.

Stomach of *Baleniceps*.

The distal end of the stomach and the pyloric chamber have been laid open to show the constriction separating the general cavity from the cavity of the pyloric chamber and the minute aperture, A, into D, the duodenum.

We have to recognize in the first place that the absence of distinction between proventriculus and gizzard gives no clue to the position of *Baleniceps* in the assemblage of Pelargo-Colymbiform birds. F. S. Leuckart (23) discussed this formation in 1841, citing the earlier authors, such as Blasius and Cuvier, who had called attention to it, described it in a number of birds and associated it with diet. It is tempting to associate such an undifferentiated condition with a primitive structure, but I do not think that such a view is tenable. At one time I myself thought that it might be possible to derive information useful for systematic purposes from the condition of the stomach, and I examined and made drawings of the organ in a large number of birds. But throughout the group, from Divers to Eagles, the extent to which gizzard may be separated from proventriculus by external or internal configuration, by specialization of muscle and tendon, or by aggregation of glandular areas, varies so irregularly as to suggest adaptation to habit rather than genetic tendency. The typical fish-eaters on the whole have a bag-like sac, weakly muscular and diffusely glandular; those that live more on flesh

or on mixed diet have the muscular portion more specialized and a tendency to the concentration of the glands. Even a formation so remarkable as the aggregation of the proventricular glands into two large circular masses has apparently little or no systematic significance. Within the group generally, the arrangement of the proventricular glands is diffuse over the whole area, but there is a tendency for them to lie in longitudinal bands, which may be numerous, as for instance in the Sea-eagles and in *Baleniceps*, or in two bands one anterior and one posterior. I found these bands rather short and rounded off in the American Grebe (*Echmophorus major*) and even more definitely rounded off in Garden's Night-heron (*Nycticorax gardeni*). The condition I described and figured for the African Tantalus (*Pseudotantalus ibis*), where the glands are in a couple of rounded bosses, and which I noted as occurring also in *Leptoptilus crumeniferus* and *L. argala*, and in *Carphibis spinicollis* (25), is obviously a simple derivative from the pair of rounded bands. The state of affairs noted by Garrod in Levaillant's Darter (20) and by Forbes in the Indian Darter (11) differs from that in the Storks only by the circular form of the two patches being a little more advanced and by a slight tendency for the circular masses to retreat into eversions of the stomach wall, a condition which is completed in *Plotus anhinga* (19) by the two patches having retreated into a rounded diverticulum. It is clear that the absence of such circular patches in *Baleniceps* tells us nothing as to the place of that bird in the system.

When I found that there was a well-marked pyloric chamber, a fact which appears not to have been recorded before, I at once remembered the existence of such a chamber in the Pelican from my own notes, and in *Plotus* from the observations of Garrod and Forbes. But as Leuckart (loc. cit.), Gadow (14), Cazin (6) and many others have shown, a pyloric chamber in varying degrees of completeness of separation occurs in many birds, notably in Herons, Storks and Darters; and even if we try to follow Cazin in limiting the term to cases where the constriction from the larger chamber is very well-marked, its presence gives no sure ground for associating *Baleniceps* more closely with any one of the groups of allied birds.

Liver.—As Beddard (3) has noted, the right lobe of the liver is very much larger than the left, a condition which he was inclined to think showed affinity with the Herons rather than with the Storks. In a later work (4), however, he states that the "relative sizes of the liver lobes appear to be of no importance systematically"—an opinion with which I concur. There is a large gall-bladder, and the cystic and hepatic ducts open nearly together, but the cystic duct distad of the hepatic duct, just beyond the end of the straight distal limb of the duodenal loop of the intestines, the disposition being very like that figured by Beddard in the case of the Indian Darter (4, p. 32) except that the hepatic duct passes through the substance of the lobulated

pancreas. On referring to my own notes, I find that a closely similar arrangement occurs in a very large number of birds belonging to widely separated groups.

Intestinal Tract.—The most notable general feature of the alimentary canal is the extremely small bulk it occupied in the body compared with the size of the bird. The actual specimen stood nearly four feet high; when the alimentary tract and mesentery had been removed by cutting the duodenum close to the stomach and the rectum close to the cloaca, the little handful of viscera placed on the dissecting board was not so large as the similar mass from a duck. The calibre of the whole tract was narrow and fairly uniform, except that the cæcum and large intestine were rather wider. The aperture leading from the stomach (*i. e.*, from the pyloric chamber of the stomach) to the duodenum was excessively small (text-fig. 121, A, p. 653); a grain of millet would have had difficulty in passing through. The minuteness of this aperture is no doubt an adaptation similar in purpose to the hair-like brush found by Garrod in *Plotus anhinga* and the similarly placed plug found by the same anatomist in Levaillant's Darter (Garrod, 19 and 20), which he surmised to be devices for preventing the passage of fish-bones into the gut.

The minuteness of the exit from the stomach and still more the further guarding of the aperture by a plug of hair-like structures may have another advantage than prevention of the passage of fish-bones. The hair-plug occurs also in the Turkey-buzzard (*Cathartes aura*), which is certainly not a habitual fish-eater. In his "Last Journal" (12) under the date Aug. 20, Forbes mentions dissecting an example of *Plotus levaillanti* and finding the stomach full of nematodes, none of which, however, had penetrated beyond the plug, although several had been caught in it. I found a number of nematodes in the stomach of my specimen of *Balaniceps*. We know now that intestinal parasites may do much damage to the animals they infest, and it is possible that the plug of hairs in the Darters and the very small exit from the stomach in *Balaniceps*, serve the useful purpose of preventing nematodes, which have been eaten with the food, from entering the intestines, keeping them in the stomach where they may eventually be killed.

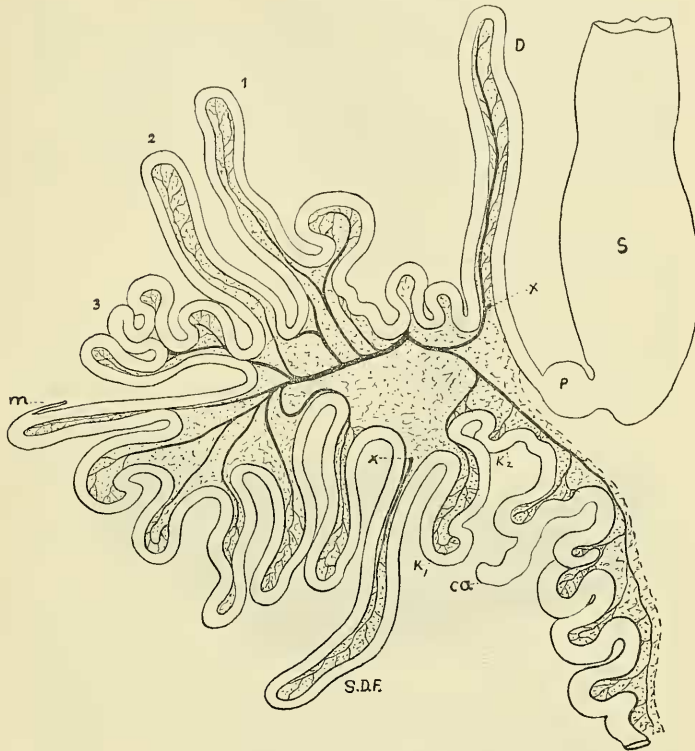
The aperture by which the distal end of the small intestine communicates with the cæcum and large intestine (text-fig. 123, B, p. 658) is only just a little larger than the opening into the duodenum. The structure of the alimentary tract shows that the Shoe-bill is adapted to make the most of a limited diet, consisting probably entirely of animal food, fish, frogs, or even small mammals; that the food must be retained for a considerable time in the stomach until it is very well macerated, for large lumps could neither enter the intestines from the stomach, nor even if they reached the intestines leave them by passing into the cæcum and large intestines. From much unpleasant experience in dissecting the alimentary tract of birds and mammals, I have learned to

note differences in the odour on the dissecting table. In the case especially of vegetarian and omnivorous creatures where the digestive tract is bulky, and large quantities of food are taken, there is usually a very offensive odour, showing that putrefaction attends the processes of intestinal digestion. In other cases, and amongst birds, notably in birds-of-prey and many fish-eaters like the Divers, the odour of the alimentary tract behind the stomach is rarely offensive, and, sometimes, even attractive and aromatic. Although I was unable to examine this specimen of the Shoebill until it had been dead for several days, the contents of the intestinal tract were not offensive.

In the figure (text-fig. 122) I represent the course of the alimentary canal, from the stomach to the cloaca, dissected out in a fashion which, as I have described in former memoirs (26, 30), seems to me to give much information as to its morphology and to afford a useful basis of comparison with the conditions existing in the different groups of birds. The secondary foldings and modes in which the gut is packed in the body-cavity are naturally not shown by this method, but the relation of the gut to the primitive mesentery, the portions of it which have been expanded into loops, and the configuration of these loops, appear with diagrammatic clearness. The first specialized loop is the duodenum; it is relatively not quite so long as in Herons generally, but it shows on its distal limb a minor expansion, represented in the drawing as two short folds, and comparable with the condition which I have figured in *Nycticorax* and *Ardea*. Then follows a second definite loop with a minor loop on its proximal limb, then a well marked loop, and then a few irregular twists, after which comes the portion bearing the remnant of Meckel's diverticulum (text-fig. 122, *m.*), the vestige of the yolk-sac, lying in the line of axis of the main branch of the portal vein. In *Balcaniceps* this was very slender, and bound closely to the inferior edge of the gut by a ventral mesentery. It might quite easily have been overlooked, if it had been sought for in the usual fashion, merely by running the gut through the fingers, but when the tract was laid out in the way I recommend, so that the blood-vessels were visible and the mesentery undisturbed, it was at once obvious. The part of Meckel's tract between this diverticulum and the usual position of the caeca is thrown first into a series of short ill-defined loops and then into a long and definite supra-duodenal loop (text-fig. 122, S.D.F.) closely attached to the duodenum in the undisturbed condition and supplied from the duodenal vein by what I have termed a "bridging" or short-circuiting vessel, which traverses the mesentery and must be cut through in process of laying out the gut (text-fig. 122 *x, x*). Then follows a rather irregular piece of gut forming two of the folds which I have described as "supra-caecal" kinks, the presence of at least one of these being characteristic of the great assemblage of birds containing the eagles and vultures, herons and storks, penguins and petrels.

Just behind the distal extremity of these kinks, the mesentery narrows so as to bring the distal end of Meckel's tract very close to the proximal end of the duodenum. This almost circular

Text-fig. 122.

Intestinal Tract of *Balaniceps*.

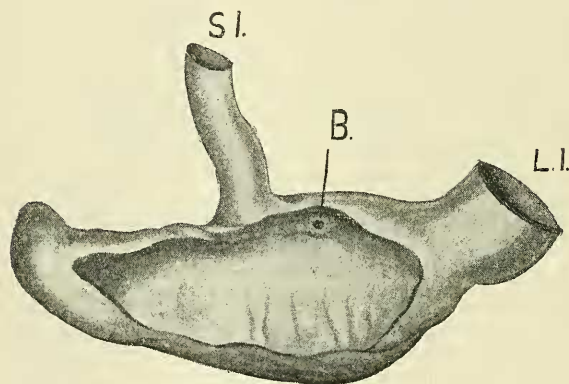
- S. Stomach.
 P. Pyloric chamber.
 D. Duodenal loop.
 1, 2, 3. The three loops of Meckel's tract anterior to the diverticulum, typical of the Pelargo-Colymbomorphine Brigade.
 m. Meckel's Diverticulum.
 S.D.F. Supra-duodenal loop.
 x, x. Cut ends of bridging vessels from duodenal loop to supra-duodenal loop.
 K1, K2. Supra-caecal kinks.
 Ca. Caecum.

expanse of mesentery grows from the simple primitive loop of which the main branch of the portal vein is the axis and which

carries the yolk-sac at its extreme point. If, as happens in many birds belonging to widely separated groups, Meckel's tract is twisted in the course of growth, the twist in the mesentery is seen here with the result that in the dissection of the gut as shown in my figures, the mesentery carrying the posterior region of the gut may be tucked or folded under the mesentery carrying Meckel's tract, so that although the two are morphologically continuous, the continuity may not be apparent except where the whole gut is short or very simple. In my diagrams, I have simplified this region, showing the morphological continuity, as the secondary twisting was not a part of my argument.

The caeca (or caecum) are to be looked for at this point, which marks the transition from Meckel's tract to the hind gut at the

Text-fig. 123.

Caecum of *Baleniceps*.

S. I. Cut small intestine.

L. I. Cut large intestine.

B. The lateral wall of the caecum has been cut away to show at B, the aperture into the small intestine, lying distally of the point where the intestine appears to pass into the caecum.

beginning of the area drained by the posterior branch of the portal vein. In *Baleniceps* only one is present, as shown in the general diagram (text-fig. 122, Ca.). The end of Meckel's tract meets the large intestine almost at a right angle, and the caecum is in continuation of the line of the large intestine. The calibre of the large intestine is rather greater than that of Meckel's tract, the difference being greater than is represented in the general diagram and rather less than in the enlarged figure (text-fig. 123), which was drawn from the specimen after it had been washed out and slightly stretched in the process of opening. The

aperture from the small intestine to the large intestine (text-fig. 123, B) is relatively extremely small and is considerably more posterior (nearer the cloaca) than the region where the one portion of the gut joins the other, the actual passage running in the conjoined walls for a certain distance. There is not more than the very slightest fold or bulge on the wall of the large intestine, which may be imagined rather than definitely stated to be a relic of an originally paired condition of the cæca.

The presence of a single cæcum in *Baleniceps* has already been noted by Forbes (10) from a prepared specimen of that region of the gut mounted in the Museum of the Royal College of Surgeons, and this specimen corresponds in every particular with the example which I have dissected and figure in this communication to the Society. Beddard, however, (3) wrote as follows:—"In the intestines I could not discover any trace of cæca at all; I believe that the single cæcum which characterizes the *Ardeidæ* (there are two in the *Ciconiæ*) may be extremely minute, and might therefore easily escape recognition in the spirit-preserved alimentary tract." I have probably examined carefully at least as many cæca of birds as any other anatomist, and Dr. Beddard's supposition seemed to me extremely improbable on general grounds. When I found that the specimen in the College of Surgeons' Museum was extremely like my own dissection, it seemed still more improbable that a structure so definite and peculiar could be present or absent in different individuals. Dr. Beddard examined viscera which had been preserved in spirit and which had been previously handled by some other investigator. On consulting with him, he was able to add to the information given in his memoir, that the late Professor Stewart was rather unwilling that so rare a specimen should be cut about too much, and he agreed with me that it was quite possible that the portion of the gut to which the cæcum is attached had been removed before he examined it. Thanks to the kindness of Mr. R. H. Burne I have now had the opportunity of comparing the gut from the example I dissected with the actual material examined by Dr. Beddard in 1888. Dr. Beddard's material was in three pieces and the greater part of the mesentery had been cut away, but enough of the latter had been left to enable me to identify with complete certainty the general disposition of the gut, to recognize the duodenal loop followed by the subsidiary loops into which the hepatic ducts open, the large loop with its proximal minor loop, exactly as in the diagram from my specimen, the short loop with the remnant of Meckel's diverticulum (which Dr. Beddard, apparently, had not noticed) in precisely the same relative position on the loop and pointing forwards, the short twists preceding the supra-duodenal loop, and the latter loop. It was evident, moreover, that the remainder of the intestinal tract had been cut away, and that Dr. Beddard had failed to find the cæcum because he had not quite the whole of the small intestine before him, and no part of the large intestine.

Examination of the preparation of the cæcum in the College of Surgeons' Museum, which Forbes had seen, as cited by Beddard in a footnote, made it most probable that that was the portion of the intestinal tract removed from the specimen Beddard examined. There is therefore no evidence in favour of Dr. Beddard's suggestion that the cæcum in *Balaniceps* may be absent, or so small as to be unnoticed.

The large intestine from the cæcum to the cloaca is relatively long in *Balaniceps* and is rather wider in calibre than the small intestine; it is thrown into a series of short irregular loops, threaded, so to say, on a mesentery which is much shorter than the course of the gut itself, and which in the usual way is drained by a large branch of mesenteric vein.

I have shown on a former occasion (30) that the characters of the intestinal tract are capable of affording a large amount of information as to the inter-relationships of the groups of birds. The primitive gut may be regarded as a tube not much longer than the length of the body-cavity it traverses and suspended from the dorsal body-wall by an antero-posterior mesentery. It is fixed at its anterior end, where it joins the stomach, at its posterior end, where it enters the cloaca, and near the middle of its length, on its ventral surface, where it is continuous with the yolk-sac. The great embryonic vein forms the chief radius of this crescentic loop, running up to the dorsal wall from the yolk-sac, and receiving a large tributary, which runs parallel with the dorsal wall, from the hind end of the body. In the course of growth the gut becomes much longer than the distance separating its anterior and posterior fixed parts, and the lengthening takes place by the outgrowth of subsidiary loops from the primitive gut. The position of these loops with regard to the fixed points of the gut, and their number and character, differ in different cases, with the result that when the alimentary tracts are laid out on the dissecting board in the fashion in which I have described, they form definite patterns. In their main features, these are constant in individuals of the same species, closely similar in the species of a genus, and show definite relationships in the families and greater groups. A type of pattern persists through the large divisions and shows a gradual increase in definiteness and specialization in the different members of these groups, with the result that the patterns can be arranged in family trees. These correspond so closely with information that can be derived from other anatomical characters, that I regard them as being an extremely useful guide to the relationships of birds. Obviously patterns are more easy to place in the system when they are highly specialized and complex, but even the shortened guts of fruit-eaters may retain marked indications of pattern.

In the great assemblage of birds which Gadow (16) has called the Pelargomorphine Legion, in which *Balaniceps* must certainly be placed, the pattern of the gut is relatively complex.

The duodenum is a definite loop, tending to be rather wide and further sub-divided in the Falconiformes, to be excessively long, twisted and rolled up with the first loop of Meckel's tract in the Ciconiiformes, to be very long, narrow and with a minor loop on its proximal limb in the Ardeiformes. In *Balæniceps*, it is not highly specialized, but the differentiation it displays is more like that in Herons than in Storks, especially in the formation of the secondary expansions at the base of its distal limb.

In the same assemblage Meckel's tract is long, and is suspended round the circumference of an almost circular expanse of mesentery which grows out from a very short portion of the primitive dorsal mesentery. It is roughly symmetrical about the main axis which runs out to the remnant of Meckel's diverticulum, the latter being invariably present. On the proximal half of the tract there is a tendency to the formation of three minor loops between the duodenum and Meckel's diverticulum. These tend to remain comparatively simple and similar in the Steganopods and in the Falconiformes. In the Ciconiiformes the tendency is for the first to become very long and secondarily twisted up with the duodenal loop, the second and third becoming nearly obliterated. In the Ardeiformes the first and second are generally rather long and definite and may form minor loops, the third is often reduced to a little bunch of small loops closely set together. In *Balæniceps* the three loops are rather more distinct than in either the Storks or the Herons, remaining in the more generalized Steganopod condition, but such differentiation as exists approaches the Ardeine pattern and shows no trace of the Ciconine peculiarities.

In the assemblage Meckel's diverticulum is actually or very nearly at the extremity of the axial loop of the tract. When it is not quite terminal, it is always on the proximal side of the loop and is then bent parallel with it, the free tip pointing proximally. The axial loop may grow out to a great relative length. These dispositions are distributed very irregularly throughout the whole assemblage which I am discussing. The axial loop, for instance, is long and has the diverticulum at the tip in some Storks and in many of the smaller Eagles and Falcons. It is short, but usually has the diverticulum at the tip in some of the Herons and in *Scopus*, *Cathartes* and *Polyborus*. It is short and bears the diverticulum proximal to its apex in *Phaethon*, *Pelecanus*, *Fregata*, *Pseudotantalus*, *Serpentarius* and *Neophron*. The latter condition exists in *Balæniceps*, and it is plain that its occurrence has no systematic significance.

In the Pelargomorphine Legion the distal part of Meckel's tract is less highly differentiated, and therefore affords fewer discriminating characters. The portion of it that follows Meckel's diverticulum is usually thrown into a bunch of short, irregular loops, and then follows a well-marked supra-duodenal loop, supplied from the mesenteric vein, and one or more definite supra-cecal kinks. In *Balæniceps*, there is first the irregular region, then a definite short loop, then a long typical supra-

duodenal loop, and then two supra-cæcal kiuks. This region supplies no definite information which might help to place *Baleniceps* inside the Legion.

In the Legion the colic cæca are much reduced and apparently practically functionless except in the Anseriformes, in most of which they are very large and functional. Although reduced in the Steganopods, they are rather less so than in the Herons and Storks and occasionally contain faecal matter. I think the presence in *Baleniceps* of a single cæcum, by no means so large as either of those in the Anseriformes, but definitely functional, communicating with the hind-gut and containing faecal matter, may be taken to be established. The presence of one cæcum, instead of the normal pair, associates *Baleniceps* with the Herons. I should be disposed to guess that the loss of one cæcum of the pair had taken place whilst both were functional, as there seems no particular reason why one of two vestigial organs should be suppressed, except as an occasional abnormality, and that the condition in the Herons, where there is a single functionless cæcum, is secondary to that in *Baleniceps*.

The characters of the large intestine in Birds generally are not sufficiently differentiated to afford much information of systematic value. There seems to have been a general tendency to the reduction of this area to an extremely short and straight course from the cæca to the cloaca, a tendency which has been independently followed by the higher members of a large number of groups. *Baleniceps* has a relatively long and capacious large intestine, and in so far has remained in a rather more primitive condition than most of the members of the Pelargomorphine Legion.

To sum up, the characters of the intestinal tract of *Baleniceps* are those of the Pelargomorphine Legion, and such specialization as it displays associates it with Ardeine birds rather than with Ciconine birds.

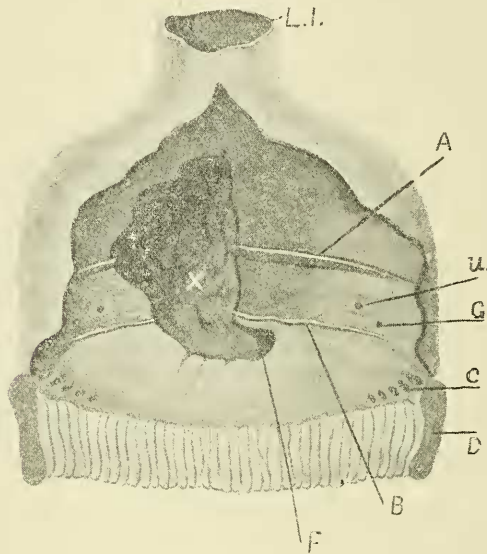
In a communication to this Society, Dr. Beddard (5) has made some additions to or corrections of my observations, particularly with regard to the presence of a specialized supra-duodenal loop in birds in which I did not record it, which are the more valuable as my work stretched over a number of years, as material was available, and it was only in its course that I began to recognize the significance of the various points and what had specially to be looked for. Dr. Beddard also on several grounds throws doubt on the value of my mode of displaying and comparing the intestinal tract patterns. These grounds are due to misapprehension. He thinks that my method of figuring the tract gives "an appearance of simplicity that is misleading, with the result that birds which are separated by marked characters are represented as being almost identical." Certainly the patterns (even if correct) do not in every case afford enough information to place clearly, or to separate clearly cases where the patterns are very simple. I was rather careful to insist on this point in

my memoir. He also thinks that I do not distinguish sufficiently between what he terms "fixed loops definitely formed by a narrow mesentery, and the irregular folds into which any mobile coil of the intestine may fall when disposed on the dissecting board." The whole tract is of course supported by mesentery, and Dr. Beddard's "fixed loops" and irregular folds are merely the beginning and final result of differentiation. The loops to which I have called attention are fixed by their morphological position, and they may be wide or narrow, long or short. More serious, however, is Dr. Beddard's misapprehension of the morphology of the gut which leads him into very curious comparisons. He states "that there are no essential differences between the intestinal tract in Birds and Crocodiles." He accepts as "perfectly correct" a diagram I gave (26, p. 137) of the alimentary tract in the Alligator, in which the canal is displayed as showing a series of almost exactly similar loops from the stomach to the cloaca, suspended on a crescentic fold of mesentery. As the pancreas lies in the first of these loops, the latter may by analogy be called the duodenum, but it is simply the first of a set of regular loops. Meckel's tract and the delimitation between that and the large intestine are not shown; it is quite clear that Meckel's tract is not differentiated. Comparison with the next figure, that of the tract in an embryonic pheasant, shows the essential difference. Immediately posterior to the duodenum a mesenteric area, corresponding to a very short length of the whole distance from the stomach to the cloaca, grows out into an enormous nearly circular tract, of which the great vein from the yolk-sac forms nearly a diameter. This region is Meckel's tract, and from the point where it returns to the dorsal line again and where the cæca, if present, are given off, the large intestine begins, and corresponds to a much larger part of the primitive distance from the pyloric extremity of the stomach to the cloaca, than the combined length of origin of the duodenum and Meckel's tract. This mode of development of the gut dominates its adult morphology. So also Dr. Beddard does not appreciate the morphological importance of the position of Meckel's diverticulum, the remnant of the yolk-sac. Fortunately it persists throughout life in most of the different groups, and its presence rules out such comparisons as Dr. Beddard makes between particular loops in *Rhea* and a Tinamu (with a Passerine intervening in the argument!). He is trying to identify different morphological material, belonging to different somites of the embryo, and this error makes his conclusions invalid. It would be of great interest to examine young chicks of those birds in which the rudiment of the yolk-sac does not usually persist, and this would clear up some of my dubious cases. But so far as they go, the gut-patterns afford an amazingly conclusive body of evidence as to the Avian system.

CLOACA.—The rectal portion of the large intestine expands suddenly to enter the large cloaca. The first chamber of the cloaca, called the coprodæum by Gadow, is separated by a thin

transverse fold (text-fig. 124, A) from the second, much narrower urodæum. The paired ureters open into the latter (text-fig. 124, U) on the dorsal surface but rather laterally placed. The actual apertures are situated on a small ridge and were very difficult to see, considering the size of the bird. I found them eventually by passing a horse-hair backwards through the ureter, and I think

Text-fig. 124.

Cloaca of *Balaniceps*. Ventral view.

The sphincter has been cut through in the middle ventral line and folded outwards; portions of the dorsal wall of the gut have been removed.

- L.I. Cut end of large intestine.
- A. Fold separating Coprodæum from Urodæum.
- B. Fold separating Urodæum from Proctodæum.
- U. Aperture of Ureter.
- G. Genital aperture.
- C. Glandular crypts.
- D. Cut sphincter muscle.
- F. Aperture of Bursa Fabricii; x, Dorsal wall of Bursa.

it possible, although I am not certain, that there were several very small apertures at each side instead of one large one. Rather lateral and slightly posterior to the ureters were the minute openings of the vasa deferentia (text-fig. 124, C). There was no genital papilla, but the specimen was a very immature male, and the testes were minute. The vas deferens accompanied

the ureter until the latter nearly had reached the wall of the cloaca, and then twisted outwards. A transverse fold also separated the urodæum from the proctodæum (text-fig. 124, B). In the proctodæum, at each side and just at the edge of the sphincter, were four or five little glandular apertures leading into small cavities lined with irregular ridges. I find in my notes of dissections of *Ostriches*, both male and female, that similar glandular crypts are present in that bird. In the middle line of the proctodæum, just behind the fold separating that chamber from the urodæum, lies the large, elongately oval aperture of the Bursa Fabricii (text-fig. 124, F). The bursa is a very large chamber, lying above the cloaca, running forwards almost to the rectum. The inner wall is lined by irregular, heavy ridges, making it resemble the reticulum of a ruminant stomach. In the figure, part of the dorsal wall of the coprodæum and urodæum is represented as cut away to show the cavity. The bursa was empty. There was no trace of a penis.

Our knowledge of the Bursa Fabricii is due chiefly to Forbes, later writers having added very little to his observations and conclusions (9). In Struthious birds, especially when they are young, there is practically no constriction separating the proctodæum and the bursa, the latter being simply a forwardly directed and dorsally placed continuation of the cavity of the posterior division of the cloaca. In the different groups of birds there appears to be a general tendency for a convergent modification of this simple arrangement; the constriction between proctodæum and cloaca becomes more and more pronounced, until the bursa becomes a tubular or pyriform sac opening by a very small pore into the dorsal wall of the cloaca. This progressive change is most marked in Passerines and in those birds in other groups which most nearly mimic the passerine type, and may lead to the complete disappearance of the aperture and of the bursa. There is of course no reasonable doubt but that the Passerines present the most specialized results of avian evolution. To a certain extent, ontogenetic changes in the bursa show a similar course of change, the aperture of the bursa narrowing, and the bursa itself tending to contract and even to disappear with age. There is probably, therefore, no special significance in the condition of the bursa in the example of *Baleniceps* I dissected, its large size and wide aperture being perhaps due to youth. Forbes, however, states that in the Storks and Herons he examined, the bursa was large and its aperture small. He also mentions the absence in these birds of the reticulum of ridges in the lining wall of the bursa, although he found them in Steganopods much as I describe them in *Baleniceps*. I cannot draw any systematic conclusions from these facts.

A small penis is stated to be present in Storks, absent in Herons, so that in the absence of that organ *Baleniceps* resembles the latter group, but I attach no systematic value to this.

MUSCULAR ANATOMY.

MUSCLES OF HEAD.

Dermo-temporalis.—This thin but extensive sheet of muscle arose at each side by a fleshy, narrow head, behind and above the temporal fossa and close to the origin of the biventer maxillæ, and spread out on the skin of the ventral surface and sides of the neck, precisely as in the Pelican.

Biventer maxillæ was very large and strong, arising from a well-marked area on the back of the head behind the quadrate and inserted to the posterior end of the lower jaw. As in the Pelican, I could not separate this from the underlying digastric or depressor mandibulæ.

Temporal.—External portion. A very strong mass, arising from the dorsal part of the temporal fossa back to the biventer; runs downwards and forwards, dipping under the ramus of the maxilla to be inserted to the outer and upper surface of the lower jaw opposite the orbit.

Pyramidal portion. Strong fan-shaped muscle arising transversely under the post-orbital process and converging to a rounded tendon which runs forwards and outwards to the inner side of the lower jaw. Parallel with this, and possibly a separate portion of it, is a flat band of muscle running from close to the articulation of the quadrate, alongside the tendon of the pyramidal portion to be inserted just anterior to it.

Quadrato-mandibular portion. Very strong fleshy muscle running transversely from the whole of the anterior surface and forward process of the quadrate to the ramus.

Quadrato-orbital portion. Long muscle from just behind the optic foramen across to the whole inner edge of the orbital process of the quadrate.

Pterygoid.—An enormous mass of muscle, partly separable into layers, on the lower surface of the jaw, from the posterior angle and ventral posterior portion of the mandible running forwards to the pterygoids.

The temporal and pterygoid muscles are practically identical with what I have found in the Pelican.

Biventer cervicis.—I examined this muscle to see if there were any trace of the peculiar formation described by Garrod in the case of the Darters, but found that the muscle with its anterior and posterior bellies was quite normal.

HYOID MUSCLES.

Mylohyoid anterior.—As in the Pelican a very slender and thin sheet of muscular fibres superficial to the other muscles of the under surface of the jaws, and running transversely across from the ramus of the jaw to spread out on the interspace between the two rami, but without meeting its fellow in a median raphæ.

Mylohyoid posterior.—Arises as a broad strap from the outer surface of the angle of the jaw just below the ear and divides into

a thin wide sheet of fibres which runs over the ventral surface, meeting its fellow of the other side and forming a platysma myoides, and a better defined band which runs across to be inserted to the ceratohyal, superficial to both divisions of the geniohyoid.

Geniohyoid.—Two well-marked divisions. A very strong division arises from the last joint and cartilaginous end of the ceratohyal, round which it is wrapped, and runs forwards to the outer surface of the lower jaw just under the orbit. The second division arises from the first joint of the ceratohyal and runs straight forwards as a sheet of fibres which meets the corresponding fibres of the same division of the other side. These fibres can be traced up to the junction of the rami of the mandible.

Genioglossus.—Probably in relation with the degeneracy of the tongue, this muscle was absent.

Ceratoglossus.—Fleshy from the outer side of the first joint of the ceratohyal to the tip of the tongue. There was no separate tendon.

The hyoid muscles, like those of the head, of *Balaniceps* were excessively like those of the Pelican, but I attach no systematic importance to the similarity, as I have very little material with which to compare these muscles in a number of different groups, and the material I have shows that, apart from obviously adaptive features, these muscles are much alike in widely separated groups.

CAUDAL MUSCLES.

Pubo-coccygeus externus.—A flat band of muscle from the posterior dorsal margin of the end of the pubis, narrowing to its insertion on the under surface of the sheath of the external rectrix.

Pubo-coccygeus internus.—This is a much wider and thinner muscle, deep of the externus, and arising from a greater area of the pubis with a reach on to the ischium. It is inserted to the hæmapophyses of the posterior caudal vertebræ.

Levator coccygis.—The two levators form a strong diagonal mass of musculature on the dorsal surface of the tail, anterior to the oil-gland. They arise from the ilium and the lateral processes of the caudal vertebræ and are inserted by a series of tendinous slips to the spinous processes of the caudals and to the membrane covering the rectrices.

Depressor coccygis.—Arises from the transverse process of the last sacral vertebra by a strong tendon just at the articulation with the ilium, and from the transverse processes of the first three free caudals; insertion to the transverse processes and hæmapophyses of the posterior caudals.

Ilio-coccygeus.—Only the outer of the two slips which usually represent this muscle is present. It arises from the ilium just dorsal to the origin of the depressor coccygis, and is inserted to the outer surface of the capsule of the external rectrix.

I have no standard for comparison in the case of the caudal muscles. The chief difference from the condition in *Leptoptilus* is the absence of the inner slip of the ilio-coccygeus.

MUSCLES OF THE SHOULDER AND WING.

Cucullaris.—The cervical portion is well developed, forming a definite sheet of circular fibres which stop abruptly in line with the proximal edge of the rhomboideus externus where they are inserted along the clavicle.

Rhomboideus externus.—Origin tendinous from the neural crests of five and a half vertebræ beginning at just opposite the junction of the scapula and clavicle. The fibres run outwards nearly transversely to all the scapula except the down-turned posterior end and forwards to part of the clavicle (text-fig. 125, Rh. 2).

Rhomboideus profundus or *internus*.—Origin tendinous, a little short of the externus proximally and reaching just beyond it distally. The fibres run outwards and backwards to no part of the clavicle but to the whole length of the scapula including the down-turned end (text-fig. 125, Rh. 1).

The two rhomboid muscles are nearly equal in thickness. These two muscles, according to Fürbringer, and my own observations confirm his view, are in process of creeping forwards. Their condition in *Baleniceps* shows a considerable degree of specialization, but I have not material to compare the condition in allied birds.

Latissimus dorsi anterior.—A broad strap of muscle arising from the anterior dorsal vertebræ only and running downwards and forwards, dipping under the anconeus, to a fleshy insertion to the shaft of the humerus distal of the insertion of the posterior division of the muscle and unconnected with it (text-fig. 125, L.A.).

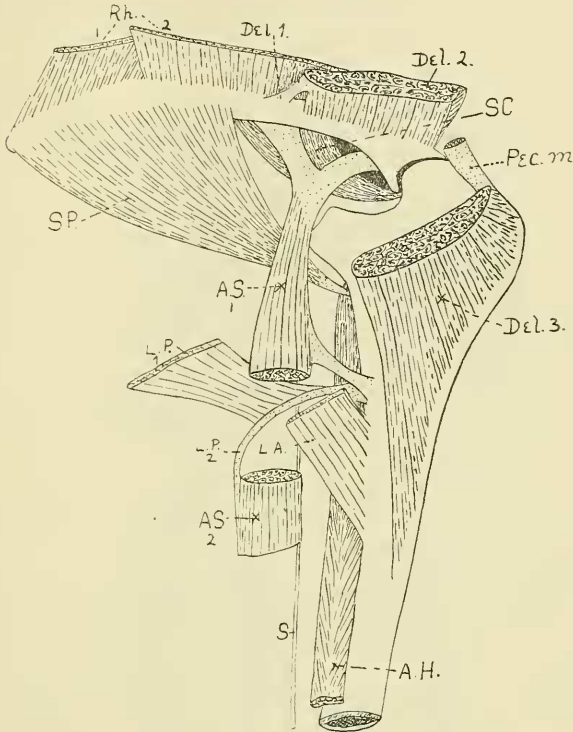
Latissimus dorsi posterior.—Fleshy origin, the anterior edge of which touches but is not fused with the posterior edge of the anterior division. Origin wider than that of the anterior division, but not reaching quite as far back as the proximal edge of the ilium. Its fibres converge to form a band about the same width as the lat. dorsi anterior (text-fig. 125, L.P. 1), pass under that muscle with a more proximal slope, to be inserted along a strong tendon (text-fig. 125, L.P. 2) which is inserted to the scapula under the scapular anchor of the anconeus, proximal to the insertion of the lat. dorsi anterior, and which joins the anconeus belly distally.

Latissimus dorsi metapatagialis.—Absent.

The anterior division is like that in *Leptoptilus*. The connection of the tendon of insertion of the posterior division with the anconeus occurs also in *Leptoptilus*, but I have noted a somewhat similar arrangement in *Bubo maximus*. The loss of the metapatagial division has been noted by Fürbringer in *Plotus*, but it is usually present in the Herons, Storks, and Steganopods.

Serratus superficialis anterior.—From the ventral end of the last cervical rib and the first dorsal rib converging to a flat

Text-fig. 125.

Shoulder-muscles of *Balaniceps*.

Right wing, external aspect. Muscle striped: tendon dotted.

- Rh. 1. Rhomboideus profundus, cut across.
 Rh. 2. Rhomboideus externus, cut across.
 Del. 1. Tendinous anchor of Deltoides major.
 Del. 2. Cut surface of Deltoides major reflected.
 Del. 3. Distal portion and insertion to humerus of Deltoides major.
 S.P. Scapulo-humeralis posterior.
 Pec.m. Tendon of insertion of Supra-coracoideus (Pectoralis minor or secundus).
 S.C. External scapular head of Sub-coraco-scapularis.
 A.S.₁. Anconæus scapularis, showing scapular origin, and anchor to humerus. It has been divided to show the Latissimus dorsi.
 A.S.₂. Anconæus scapularis, part of the belly.
 A.H. Anconæus humeralis.
 L.A. Latissimus dorsi anterior, insertion.
 L.P. 1. Cut edge of Latissimus dorsi posterior.
 L.P. 2. Tendon of insertion of Lat. dorsi posterior from humerus to junction with Anconæus scapularis.
 S. Vestige of Expansor secundariorum. The distinctness of this is exaggerated in the drawing.

tendon which is inserted to the postglenoid scapula between the two parts of the sub-coraco-scapularis, its insertion being quite covered by the outer part of that.

Serratus superficialis posterior.—From the first two uncinate processes and area of their ribs in line with them to about three-quarters of an inch of the posterior inferior border of the scapula; covered by the third portion of the serratus superficialis.

Serratus superficialis metapatagialis.—Origin from the same two ribs as the ser. super. posterior, but entirely from below the uncinate processes, and reaching down almost to the sternum. Insertion to the metapatagium, with a strong tendinous slip to the tip of the scapula.

The first of the three serrati, according to Fürbringer, is very variable even within families. The second is constant in many families, variable in others. The limitation of the origin to dorsal of the uncinates is somewhat rare but has been noted in *Phœnicopterus*. The insertion of the serratus metapat. partly to the scapula appears to be extremely rare. Fürbringer has noted it in *Crex*, where the condition is much as I find it to be in *Balæniceps*, and in *Fulmarus* and *Bucorvus*, where the scapular insertion alone occurs. The relation to the scapula is probably a vestige of the origin of this muscle as a separated portion of the serratus superfic. posterior.

Serratus profundus.—From the last two cervical and first two dorsal ribs to the scapula in four digitations. According to Fürbringer, this arrangement is normal in *Herodii*.

Biceps brachii.—This arises by a flat narrow tendon from the acrocoracoid (text-fig. 128, B. 1, p. 675), alongside but not covered by the origin of the coracobrachialis externus and separated by that muscle from the tendon of insertion of the supracoracoideus (pectoralis secundus). It passes under the insertions of the pectoralis major without being connected with them, and passing into a rounded belly (text-fig. 128, B. 2) runs down parallel with the humerus to be inserted to a knob on the ulnar face of the radius (text-fig. 127, Bi., 1, p. 672). It is then continued across to the opposite face of the ulna (text-fig. 127, 4, 5) by a deep broad tendon and a narrow more superficial tendon, first sending a strong slip (text-fig. 127, 2) to the radial end of a radio-ulnar ligament.

The biceps obviously presents a highly specialized condition in *Balæniceps*, the specialization consisting of the complete loss of the usual humeral head. The two divisions are well separated at their origin, and the radial and ulnar tendons of insertion separate rather high up in most Steganopods, Storks and Herons. As Fürbringer has pointed out, the humeral head in such cases can be traced to the radial insertion. As both radial and ulnar insertions are well marked, indeed rather unusually complex in *Balæniceps*, I infer that the loss of the humeral head is comparatively recent.

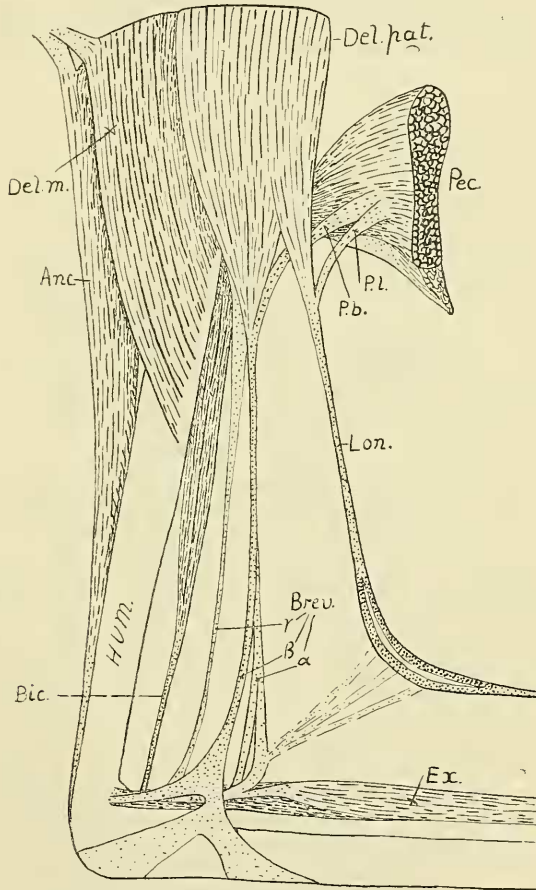
Biceps patagialis.—This slip to the patagial tendons is absent

in *Baleniceps*, as in Storks, Herons, *Scopus*, and most Steganopods. The absence, however, is not of much value; the slip is present in some Steganopods, in Spoonbills, in *Phaenicopterus*, and is present or absent within the same family in a number of cases.

Deltoides propatagialis (text-fig. 126, Del. pat.).

I have already mentioned that there is no biceps propatagialis.

Text-fig. 126.



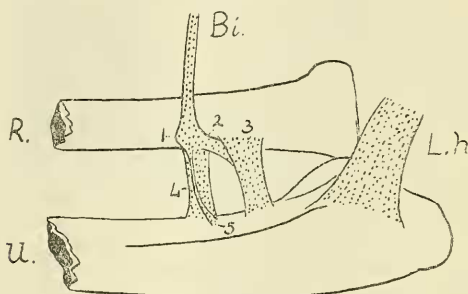
Patagial muscles and tendons of *Baleniceps*.

Del.m. Deltoides major. Anc. Anconæus scapularis. Hum. Humerus. Bic. Biceps. Del.pat. Deltoides propatagialis. Pec. Pectoralis major cut across. P.l. Pectoralis slip to longus tendon. P.b. Pectoralis slip to brevis tendon. Lon. Longus tendon. Brev. Brevis tendon with the slips named α , β , and γ by Fürbringer. Ex. Extensor metacarpi radialis.

There is no cucullaris propatagialis. The patagial tendons arise solely from the deltoides propatagialis and from the pectoralis propatagialis, and there are no anchors to the humerus.

The origin of the deltoides patagialis is from the clavicle, acrocoracoid ligament and part of the scapula, the latter origin not being found in Herons. Distally it splits into two peaks, a smaller from which the longus tendon arises and a larger for the brevis tendon. This is a more specialized condition than in Steganopods, Storks and Herons generally, where even the longus and brevis tendons have a short common course, but in *Scopus* and *Leptoptilus* there are separate peaks for the tendons.

Text-fig. 127.



Insertion of Biceps ligament.

R. Radius. U. Ulna. Bi. Biceps tendon: 1, insertion to radius; 2, insertion to radio-ulnar ligament; 4, insertion to ulna; 5, second superficial insertion to ulna; 3, radio-ulnar ligament. L.h. Humero-ulnar ligament.

The longus tendon (text-fig. 126, Lon.), after being reinforced by a slip from the pectoral, enlarges in width and becomes elastic, this portion being doubled, and being anchored by a very faint (much fainter and more diffuse than would appear from the drawing in fig. 126) set of fibres from the distal portion of the brevis.

The brevis tendon (text-fig. 126, Brev.) is highly specialized. The main mass of the muscle passes into a strong rounded tendon which is reinforced by the pectoralis slip and represents the conjoined α and β slips of Fürbringer, the beta slip being the direct continuation of the muscle, but giving off half-way down the patagium a broader and weaker alpha slip. The latter itself becomes doubled distally, gives off a weak anchor to the elastic portion of the longus tendon and is inserted to the extensor metacarpi radialis tendon. The beta slip broadens out as it reaches the fascia over the extensor, sends forward a stout anchor which covers and is fused with the tendinous head of the extensor metacarpi, and sends downwards a branch which forms a forked fan reaching the distal edge of the forearm. The gamma slip of

Fürbringer is the most proximally placed, and is distinct although very flat and weak throughout its whole length from its origin at the proximal side of the brevis muscular peak to its insertion to the recurrent beta slip.

The course of evolution of the brevis tendon appears to have been from a wide rather diffused band to first a specialization of portions of that band into the slips distinguished by Fürbringer, then to a separation of these slips, and finally to the loss of one or more of them. In the Storks, Herons and *Scopus* the slips are at least separate distally; in Storks and Herons the separation of alpha and beta is only distal and does not begin so high up as in *Baleniceps*, in which, although the actual separation occurs only about half-way down the patagium, the identity of beta can be traced right up to its origin. Beddard figures an almost similar condition for *Scopus* (2, fig. 2). So also the very complete separation of gamma and beta occurs in *Scopus* and *Baleniceps*, and is much less distinct except distally in Storks and Herons. The resemblance between *Baleniceps* and *Scopus* appears to be rather close; the most important differences being the greater distinctness of the anchor to the longus in *Scopus*, and the presence of an anchor to the humerus in the same bird.

Deltoides major (text-fig. 125, Del. 1, Del. 2, Del. 3, p. 669; text-fig. 126, Del.m.; text-fig. 128, De.).—This large muscle arises fleshy from the scapula but with a distal tendinous anchor just external to that of the anconeus, and is inserted fleshy to nearly half-way down the humerus. It is very nearly divided into the two portions visible in *Leptoptilus* and other storks. The tendinous anchor occurs in the Herons and Storks that I have dissected, and Beddard has recorded it in *Scopus*.

Deltoides minor.—This muscle, possibly owing to the large size of the *deltoides major*, is not to be distinguished as a separate muscle: probably it is absent. In Storks it is small and quite separate.

Scapulo-humeralis anterior.—This small muscle is absent. In Steganopods, Storks and Herons it lies very close to the *teres major*, so that it is possible that it may have fused with this in *Baleniceps*. Beddard does not mention it in his description of the shoulder muscles of *Scopus*, so that possibly it may also be absent in that bird.

Scapulo-humeralis posterior (Teres major) (text-fig. 125, SP).—A strong but relatively rather small muscle arising from about the distal half of the scapula and inserted to the humerus between the two heads of the anconeus. A relatively narrow insertion, according to Fürbringer, also occurs in Steganopods, Storks and Herons. In *Baleniceps* it has no accessory anchors or attachments.

Sub-coraco-scapularis.—The coracoid head (*Coracobrachialis brevis* of Garrod) is single and much smaller than the scapular heads. It arises only from the proximal half to third of the inner face of the coracoid, as in Storks and Herons, and converges

to join the scapular heads near their tendon of insertion. The external (text-fig. 125, S.C., p. 669) and internal scapular heads arise from about the second fifth of the under surface of the scapula, where they are separated by the insertion of the serratus superficialis anterior. The three heads unite to form a strong rounded tendon inserted to the median tubercle of the humerus.

Anconæus.

Anconæus scapularis.—Origin by a strong forked tendon from scapula (text-fig. 125, A.S. 1, A.S. 2), passes into a rounded muscular belly which sends an anchor to the humerus near the insertion of the latissimus dorsi and receives a strong tendon from the latissimus dorsi posterior. Passes into a strong flat tendon just before reaching the elbow.

Anconæus humeralis (text-fig. 125, A.H.).—Origin from the whole length of the humerus, the origin being cleft proximally. Passes into a tendon at the distal end of the humerus, and this runs parallel with but united only by membrane to the tendon of insertion of the anconæus scapularis. Insertion to the olecranon of the ulna.

The forked head of the scapular portion, the anchor to the humerus, and the general relations of the two divisions of the muscle are very much like what I have observed or find recorded in Storks and Herons. The absence of any extension of the scapular head to the clavicle or coracoid is rather a primitive feature.

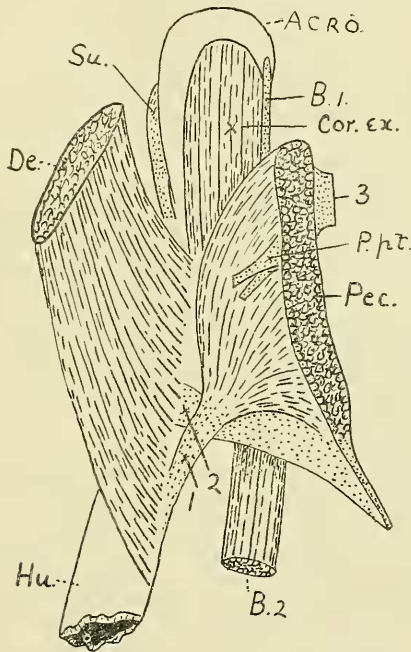
Anconæus caput coracoideum (Expansor secundariorum) (text-fig. 125, S.).—At the elbow there was a slip of muscular fibres connected with the feathers and giving rise to a very delicate tendon which I traced up the under surface of the skin close to the anconæus, but which then appeared to become diffuse and be lost in the subdermal fasciæ. There was no trace of it passing through the edge of the teres major, as usually happens when it is well developed, or in the axilla.

This was one of the muscles to which Garrod paid great attention, hoping to find it useful in classification, but further observations have not justified his anticipations, as it is present or absent in very closely allied birds. It is usually absent in Steganopods, but present in a few cases. It is present in Storks, and in Herons except *Ardetta* and *Canceroma*. According to Beddard it is absent in *Scopus*. Its vestigial presence in *Balcaniceps* is therefore interesting but of no systematic value.

Pectoralis thoracicus.—The great pectoral (text-fig. 126, Pec., p. 671; text-fig. 128, Pec.) in *Balcaniceps* is an enormous mass of muscle arising from the clavicle, the membrane between the clavicle and coracoid, from the whole of the keel and from all the posterior part of the sternum with a considerable overlap to the ribs. I could not trace any definite horizontal division of the muscular mass. The insertion is by two very distinct tendons, which cross each other in a remarkable fashion. The greater and more

proximal mass of the muscle converges to a strong flattened tendon (text-fig. 128, 1), which is inserted to the humerus rather distally and not far from the posterior end of the deltoid insertion. The more distal portion of the muscle converges to a much broader tendon, which forms the posterior border of the whole muscle and then dipping under the first tendon of insertion runs in to the humerus proximally of it (text-fig. 128, 2). There is also a strong anchor to the humerus, shown as cut and reflected in the figure (text-fig. 128, 3).

Text-fig. 128.



Pectoral muscle of *Balaniceps*. Tendon dotted; muscle striped.

ACRO. Acrocoracoide process. Hu. Humerus.

Pec. Pectoralis major, cut across.

1, 2. Insertion tendons of pectoralis to humerus. 3. Anchor to humerus, divided and reflected.

P.pt. Pectorales propatagiales.

Su. Tendon of insertion of supracoracoideus (Pect. minor).

De. Deltoides major.

Cor. ex. Coracobrachialis externus.

B. 1. Tendon of origin of biceps. B. 2. Cut belly of biceps.

The large area of origin of the great pectoral is of course associated with a powerful wing, and is probably purely adaptive

The strong proximal anchor (text-fig. 128, 3) to the humerus also occurs in many Steganopods, in Storks, Herons, and is probably represented in *Scopus*, in which bird Beddard mentions a strong insertion to a fibrous aponeurosis attached to the crista of the humerus and covering the biceps. It is characteristic of Storks as opposed to Herons, that in the former birds the great pectoral is completely divided into two muscles, as it is in the Pelican and some other Steganopods. The insertions of these portions as described by Weldon correspond almost exactly with the double insertion in *Balæniceps*, and I was able to separate the mass of muscle quite easily into portions corresponding with these insertions, although, in the absence of the separate insertions, I should not have described the muscle as doubled. But, whatever the distinction be worth, the great pectoral muscle of *Balæniceps* is more Ciconine than Ardeine. Beddard's description of the condition in *Scopus* is not sufficiently detailed to follow in this matter, but he speaks of it as "partly doubled," and the humerus shows marks of a double insertion.

Pectoralis propatagialis (text-figs. 126, 128, pp. 671, 675).—As I have already stated, there are separate slips from the pectoral for the longus and brevis tendons. Both slips are entirely tendinous, and that for the longus is smaller and more superficial (text-fig. 126, P.l., P.b.; text-fig. 128, P.pt.). In my dissections of Herons, I find similarly distinct slips for the brevis and longus from the pectoral; Beddard mentions them for *Scopus*, but in the case of Storks the usual arrangement appears to be the more primitive condition of a single slip, which joins the patagial tendon before that has divided into longus and brevis.

Pectoralis abdominalis.—This is absent in *Balæniceps* as in Storks. It is present in Herons, but Beddard does not refer to its presence or absence in the case of *Scopus*.

Supracoracoideus (*Pectoralis minor*).—This is a small and rather narrow muscle elongately oval, with a centrally placed tendon like the mid-rib of a leaf. Its fleshy origin is limited to a very small part of the sternum, including no part of the keel, and part of the coracoid and the membrane between the coracoid and clavicle. It is widely separated on the coracoid from the origin of the *coracobrachialis posterior* (*pectoralis tertius*) and its tendon of insertion (text-fig. 128, Su.) is free from any fibres that could represent a *deltoides minor*. Its general relations and small size are closely paralleled in Herons and Storks.

Coracobrachialis externus or *anterior*.—A strong muscle arising fleshy from the acrocoracoid only (text-fig. 128, Cor. ex.) and covered only at the extreme edge by the tendon of origin of the biceps. Insertion on a broadly oval area to the planum bicipitale of the humerus.

Coracobrachialis internus (*Pectoralis tertius*).—A very stout almost doubled mass of muscle from the distal dorsal two-thirds of the edge of the coracoid opposite the origin of the supracora-

coideus, but quite separate from that. Its fibres converge to a strong tendon inserted to a peak of the median tubercle of the humerus.

MUSCLES OF FOREARM AND NECK.

Brachialis inferior.—A very strong flat sheet of muscle with a fleshy origin and insertion, occupying the angle between the humerus and ulna, the insertion to the ulna being twice the width of the origin from the flexor aspect of the humerus.

Pronator sublimis or *brevis*.—Short muscle from the inner condyle of the humerus to the first quarter of the radius. This insertion is rather shorter than in *Leptoptilus*.

Pronator profundus or *longus*.—As in *Leptoptilus* a larger muscle, from the inner condyle of the humerus to a little beyond the surface of the radius covered by the *brevis* and more on the ulnar aspect than the *brevis*.

Ectepicondylo-ulnaris.—Absent, as in *Leptoptilus*, but according to Gadow present only in *Rasores* and *Tinamus*.

Ectepicondylo-ulnaris.—From outer condyle of the humerus to first third of ulna on its radial face. A very thick and strong muscle, closely united with the flexor digitorum profundus. As in *Leptoptilus*.

Ectepicondylo-radialis.—A thin muscle arising by a flat tendon from the outer condyle of the humerus along with the extensor digitorum communis, inserted to a quarter of the radius; as in *Leptoptilus*, except that the insertion is shorter in the latter bird.

Flexor carpi ulnaris.—From the inner condyle of the humerus with a sesamoid; runs down the inner surface of the ulna to the great tuberosity of the ulnar carpal. Arising as a fleshy belly a thinner tendon connected with the quills runs down to end on the carpal alongside the great tendon. As in *Leptoptilus*.

Ulni-metacarpalis ventralis.—Fleshy from the last third of the ulna on the radial face; tendon crosses over a slide on the radial carpal and is inserted on a hump of the second metacarpal near the attachment of the pollex.

Ulni-metacarpalis dorsalis.—Short muscle arising by a tendon from the distal end of the ulna on its lateral face; it divides into a shorter portion running straight across to the upper part of metacarpal III and a broader portion inserted to about two-thirds of the upper surface of metacarpal III, where that is free. Similar in *Leptoptilus*, except that the first portion is tendinous, the second fleshy, while both are fleshy in *Baleniceps*.

Extensor metacarpi radialis.—Two heads, outer tendinous, inner fleshy, from the outer condyle of the humerus. The outer belly is quite separate from the inner belly and is connected with the *brevis* tendons of the patagium (text-fig. 126, Ex., p. 671). Insertion to the base of metacarpal I, the tendons from the two

bellies remaining separate until their insertion, so that the muscle is completely double. In *Leptoptilus* the tendons fuse distally.

Extensor metacarpi ulnaris.—Arises from the external condyle of the humerus by a tendon superficial to that of the ectepicondyloulnaris; then a long fleshy belly, then a thin tendon passing over a groove in the distal end of the ulna from which it receives a strong anchoring slip, absent in *Leptoptilus*, to its insertion on metacarpal II just where metacarpal III is given off.

Flexor digitorum sublimis.—A strong band of tendon runs from the inner condyle of the humerus to the ulnar carpal, from the upper side of which the flexor digitorum sublimis arises as a delicate fleshy muscle giving rise to a slender tendon which passes over a groove in the ulnar carpal and is inserted to the base of phalanx 2 of digit II, but with first an insertion to the base of the first phalanx of that digit, which I do not find recorded in my notes on *Leptoptilus*.

Flexor digitorum profundus.—Arises fleshy from the second and third fifths of the ulna, very closely connected with the insertion of the ectepicondyloulnaris. The tendon begins where the origin from the ulna ceases, and runs down the radial face of the ulnar carpal under the ligament from the radius to metacarpal II, and then follows the tendon of the superficial flexor to be inserted just beyond it to phalanx 2 of digit II. It receives a strong slip from the short extensor of the thumb, which I did not record in the case of *Leptoptilus*. Gadow mentions somewhat similar relations with the thumb in the case of Owls and *Heliornis*.

Extensor digitorum communis.—Arises tendinous from the external condyle of the humerus and passes into a slender belly a quarter way down the forearm, but receives no fibres from the ulna. Its tendon of insertion passes through a groove in the end of the ulna and then sends a branch to the base of phalanx 1 of digit I and a stronger tendon to phalanx 2 of digit II. As in *Leptoptilus*.

Extensor pollicis longus.—Two slender fleshy heads from the adjacent surfaces of the radius and ulna at their proximal ends, with accessory fibres from a large part of the length of the radius on its ulnar face. Tendon unites with that of the extensor metacarpi radialis at its insertion. As in *Leptoptilus*.

Extensor indicis longus.—One head fleshy from the distal half of the radius and a second much smaller, tendinous from the distal end of the radius and from radial carpal. Insertion to the second phalanx of digit II, but attached by fascia to the first phalanx. As in *Leptoptilus*.

Interosseus dorsalis.—Arises fleshy from the opposite faces of metacarpals II and III; fibres run to a centrally placed tendon, like the midrib of a leaf, and this is inserted to the base of the second phalanx of digit II. As in *Leptoptilus*.

Interosseus palmaris.—More ventral and stronger than the foregoing muscle but with similar origin and arrangement.

Tendon inserted to phalanx 2 of digit II. In *Leptoptilus* I have noted it as reaching only the first phalanx.

Abductor indicis.—Strong muscle arising fleshy from the whole of the radial side of metacarpal II. Inserted to the base of the phalanx 1 of digit II. As in *Leptoptilus*.

Flexor digiti III.—Arises fleshy from the ulnar side of metacarpal III and is inserted to the base of the first phalanx of the corresponding digit. As in *Leptoptilus*.

Adductor pollicis.—A strong muscle from the metacarpal to the tip of the pollex.

Extensor pollicis.—This muscle, which is usually described as single, is represented by two distinct and well-developed muscles, a condition which has been described in the case of *Struthio*, but not in other birds. Most probably, if it were carefully looked for, it would be found elsewhere. The first of the two is a strong slip from metacarpal I and the tendon of the extensor metacarpi radialis to the radial side of the thumb. It is this muscle that gives off a slip to the flexor digitorum profundus. The second muscle is from the head of metacarpal II to the base of the thumb.

MUSCLES OF THE THIGH AND LEG.

Ilio-tibialis internus (Sartorius).—A large and strong strap arising from the anterior and lower border of the ilium and from the fasciæ over the gluteus medius, and closely united along its distal border with the gluteus maximus. Normal insertion to the tibia. I find no notable difference as compared with Storks and Herons.

Ilio-tibialis (Gluteus maximus).—The origin is entirely tendinous and a median tendinous area separates the fleshy anterior and posterior borders. Posteriorly the origin extends backwards half-way over the origin of the biceps, that is to say what Garrod called the post-acetabular part of the muscle, the ilio-tibialis posterior, is present. Garrod tried to use the presence or absence of this in his systematic arrangements, but without much success. It is absent in the Steganopods generally, usually absent in Storks but present in *Ciconia*, absent or very slightly developed in Herons. So far as I can judge, the presence of the post-acetabular portion of this muscle is a primitive condition, and it has been lost or reduced independently in many groups of birds.

Ilio-trochanterici.—The externus (text-fig. 129, Gl. 1) and the posterior (text-fig. 129, Gl. 2) are both present in the normal condition. The minimus and quartus are represented by a single tendon of origin and muscular belly (text-fig. 129, Gl. 3). In *Leptoptilus* I found these quite distinct in their origin and insertion; in *Nycticorax* they had a common tendon to the femur but separate insertions to the ilium. These muscles, however, vary so much from bird to bird that I cannot attach any significance to their distinctness or fusion.

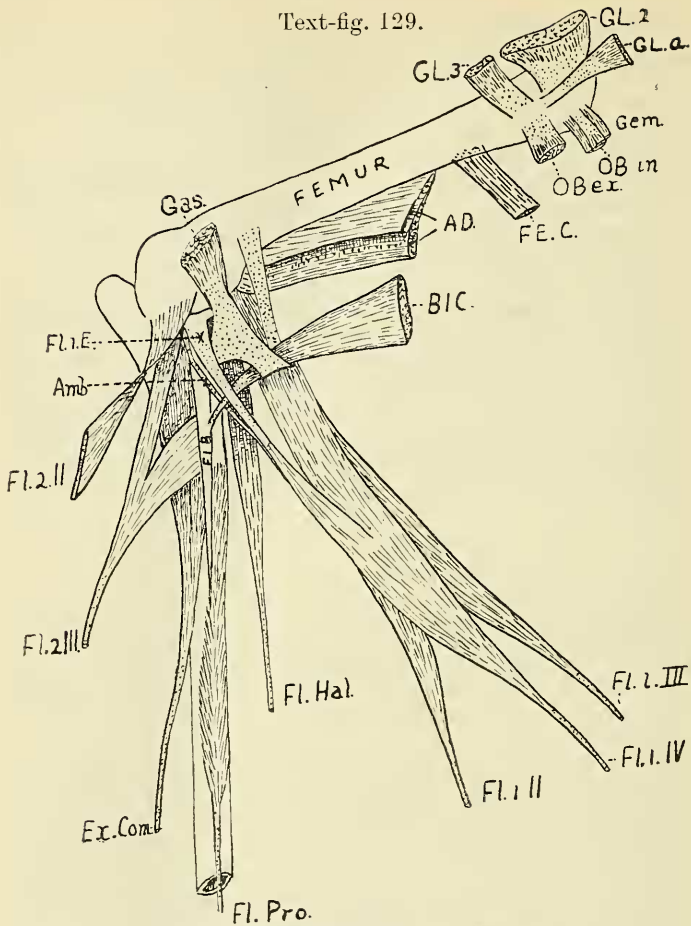


Diagram of Muscles of the leg in *Baleniceps*.

Left leg, external aspect. Tendon is dotted.

FEMUR. Femur. FIB. Fibula.

GL. a. Ilio-trochantericus externus (Gluteus anterior). GL. 2. Iltroch. posterior (Gluteus minor). GL. 3. Iltroch. anterior et medius (Gluteus minimus and quartus).

Ob. ex. Obturator externus.

Ob. in. Obturator internus, surrounded by Gem., Gemellus.

F.E.C. Origin of Femoro-caudal.

A.D. Adductor longus (the upper muscle) and Adductor magnus.

BIC. Insertion of Ilio-fibularis or biceps, passing through a sling.

Gas. External head of Gastrocnemius, cut and reflected to show relation to short arm of the Biceps sling.

Fl. 1.II, Fl. 1.III, Fl. 1.IV. Tendons to respective toes of the Perforated Flexor muscles.

Amb. Ambiens head of Perforated Flexors.

Fl. 1.E. External head of Perforated Flexors.

Fl. 2.II, Fl. 2.III. Perforated and Perforating Flexors of digits II & III.

Fl. Hal. Flexor longus hallucis.

Fl. Pro. Flexor profundus.

Ex. Com. Extensor communis.

Ilio-femoralis internus (Pectineus).—Strong, little fleshy slip from the ventral edge of the preacetabular portion of the ilium to the back of the femur below the neck. As in most birds.

Femori-tibiales (Crureus and Vastus).—The external muscles are fused to form a common mass; the vastus internus is large, arising from nearly the whole length of the femur.

Caud-ilio-femoralis (Femoro-caudal).—This is a broad thin strap of muscle arising fleshy from the femur (text-fig. 129, FE.C.) and running upwards and backwards under the biceps and between the semitendinosus and the semimembranosus and passing to the underside of the tail, where it becomes a thin tendon spreading out into a sheet which meets its fellow of the other side, the combined insertion being to the tendon of the depressor coccygis where that is inserted to the hæmapophyses of the posterior caudal vertebræ. There is no accessory femoro-caudal. The accessory fem.-caud. is, I believe, invariably absent in Steganopods, Herons and Storks, although it is present in Spoonbills and the Flamingo. The fem.-caud. itself tends to be degenerate. It is usually present in Storks, but is very slender in *Dissura* and absent in *Leptoptilus*; it is weak in the Herons and absent in several genera.

Caud-ilio-flexorius (Semitendinosus and Accessory semitendinosus).—Origin fleshy from the ischium behind the biceps and extending on to the fascia posterior to the ischium; meets the rather small but distinct accessory or femoral head in a tendinous raphe, and the combined muscles are inserted to the middle belly of the gastrocnemius (text-fig. 130, C.II. 1 & 2). The muscle is much weaker than the semimembranosus.

Ischio-flexorius (Semimembranosus).—This is the usual broad strap underlying the semitendinosus, and in this case much thicker and wider than the latter. It has a wide origin from the lower edge of the ischium and the fascia over the obturator externus, is unconnected with the semitendinosus, but receives a strong tendinous slip (text-fig. 130, Sl.) from the inner adductor and then is inserted to the tibia by a flat tendon.

Gastrocnemius.—There are the usual three heads of which the tibial head is the strongest. The outer head arises from the external condyle of the femur in common with the short arm of the biceps sling (text-fig. 129, Gas.). The middle head is the smallest and arises from between the condyles of the femur by a flat tendon. The tibial head is enormous and arises from the tendon of the ilio-tibialis and from the cnemial crest of the tibia. The three heads unite in the usual way rather less than half-way down the leg to form the tendo achillis.

Relations of the Caud-ilio-flexorius, Ischio-flexorius, and Gastrocnemius.—Weldon (38) called attention to the varying relations of these muscles and the differences they presented in Storks, Ducks, and *Phœnicopterus*. I have noted them in a number of Storks and Herons and paid a good deal of attention to them in Gruiform and Limicoline Birds (31 & 32). With minor variations as to the precise interconnections of the

semitendinosus and semimembranosus, the condition which I found in *Baleniceps* seems to be typical in Herons and Storks (text-fig. 130). The middle head of the gastrocnemius is joined by the semitendinosus just after the latter has been met by its accessory. The accessory origin from the femur is parallel to but separate from that of the middle head. The accessory is present in Herons, Storks, *Scopus*, and in *Baleniceps*; it is frequently absent among the Steganopods. In my opinion the middle head of the gastrocnemius is a separated portion of the accessory semitendinosus, and separation of the two, with subsequent disappearance of one or of both, is a secondary or specialized condition.

Ilio-fibularis (Biceps).—Very strong fleshy origin from the whole of the post-acetabular ridge of the ilium to the beginning of the origin of the semitendinosus. The strong belly converges to a rounded tendon which is inserted to the fibula after passing through a sling in the usual way (text-fig. 129, BIC.). The short arm of the sling has a strong anchor to the fibula, which I happen to have noted in Herons, but which is present also in many birds belonging to widely separated groups.

Ischio-femoralis (Obdurator externus).—Arises by strong tendon from external condyle of the femur (text-fig. 129, Ob.ex.) and inserted fleshy to surface of the ischium.

Obdurator (Obdurator internus).—Origin by a strong tendon surrounded by a gemellus muscle (text-fig. 129, OB.in.Gem.) from the external condyle of the femur proximal to the obdurator externus. Garrod (18) believed that in most cases the insertion of this muscle to the inner aspect of the pubis and ischium could be distinguished as oval or triangular, and attached some systematic value to the condition. He described it as oval in Steganopods and Storks and triangular in Herons; in *Baleniceps* it is plainly oval.

Pub-ischio-femorales (Adductor longus and Add. magnus).—The external or longus is only about half the width of the inner or magnus, but their origins and insertions are practically co-extensive. In my notes I find that they were nearly equal in Herons and Storks, but I have not paid special attention to the point. The slips from the magnus to the tibia (text-fig. 130, Sl.) and the slip to the semimembranosus (text-fig. 130) I have not noted in Storks or Herons.

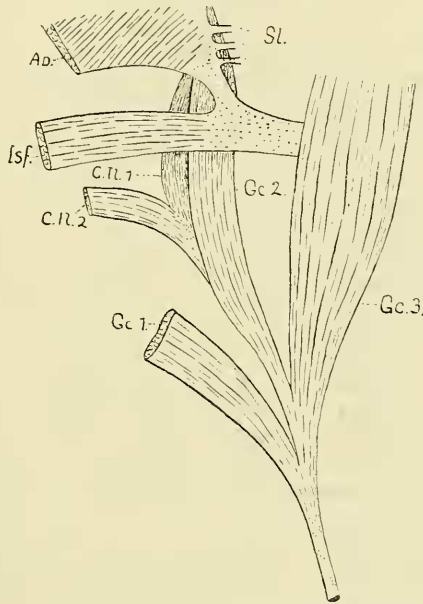
Peroneus superficialis (longus).—Strong muscle from crest of tibia and fascia over the tibialis anticus; usual insertion by broad tendon to the fascia of the ankle and a long tendon running down to join with the tendon of the perforated flexor of the third toe. Precisely the same relations exist in Storks and Herons, but also in so many other birds that no systematic importance can be attached to them.

Peroneus profundus.—A short but stout muscle from the tibia below the fibula; its tendon passes over the ankle-joint to be inserted to a knob on the outer side of the tarsus-metatarsus.

According to Weldon and my own notes, this muscle is absent in *Leptoptilus*, but I found it present and with an extension of its origin to the fibula in Herons.

Tibialis anticus.—The outer head arises by a strong tendon from the external condyle of the femur and runs in a deep groove to join the fleshy head from the tibial crest. Insertion by a forked tendon to the tarsus-metatarsus, in a pit about an inch below the joint. The conditions are practically the same in Herons and Storks.

Text-fig. 130.

Gastrocnemius and its relations in *Balæniceps*.

- Ad. Adductor magnus Sl. Tendinous slips from adductor to tibia.
 Isf. Ischio-flexorius (Semimembranosus).
 C. Il. 1. Femoral head of Caudilio-flexorius (Accessory Semitendinosus).
 C. Il. 2. Belly of Caudilio-flexorius (Semitendinosus).
 Gc. 1, external, Gc. 2, middle, Gc. 3, tibial portion of Gastrocnemius.

Soleus.—This little muscle has the usual relations, but is relatively rather stronger than in Storks and Herons; it arises fleshy from the inner side of the tibia and is inserted to the annular cartilage of the ankle-joint.

Extensor communis digitorum: arises fleshy from the crest and external surface of the shaft of the tibia (text-fig. 129, Ex.com.). The strong tendon passes through a bony and a fibrous bridge and runs down to the digits where it divides symmetrically into

two, each branch again dividing into two, the four tendons running respectively to the second digit, to each side of the third digit and to the fourth digit. The arrangement is practically identical in Storks and Herons.

Flexor perforans et perforatus (Flexor secundus) of digit II.—Origin is from the external condyle of the femur distal to the short arm of the biceps sling (text-fig. 129, Fl. 2 II, p. 680) and from the fascia over the knee-joint, immediately superficial to the corresponding flexor of the third digit with which it is closely connected. The tendon passes in the normal fashion to the second digit, perforating the tendon of the flexor primus and being perforated by the branch of the tendon of the flexor communis.

Flexor perforans et perforatus (Flexor secundus) of digit III.—This has two heads, one just deep of the corresponding flexor of the second digit and practically common with it, and a second from the edge of the fibula. Its tendon receives a strong slip from the tendon of the perforated flexor (flexor primus) of its own digit and then is inserted to digit III in the same fashion as the corresponding flexor of digit II. I did not record the existence of the second head of this flexor in my notes on Storks and Herons, but otherwise the flexores secundi have identical relations in *Baleniceps*, Storks and Herons. It must be noticed, however, that these relations are found in a very large number of birds belonging to different groups.

Flexores perforati (Flexores primi) of digits II, III, IV; Rudiment of *Ambiens*.—The perforated flexor muscles (text-fig. 129, Fl. 1. II, Fl. 1. III, Fl. 1. IV) are very closely united. Distally the tendons for the respective digits separate out; proximally the common muscular belly arises from three distinct heads and the arrangement is such that fibres to each tendon can be traced to each head. The largest head is fleshy from the intercondylar notch of the femur; there is an outer rather broad tendinous head, superficial to the biceps tendon and arising from the head of the fibula (text-fig. 129, Fl. 1. E). The third head is a round and very distinct tendon, passing under the biceps tendon and running partly to the head of the fibula and partly to the fascia of origin of the flexores secundi (text-fig. 129, Amb.). The inner fleshy head is normal and occurs in practically identical form in all birds that I have dissected. The outer tendinous head also is usually present, and exists in Storks and Herons, the chief differences it presents being in the extent to which it is muscular. In *Baleniceps*, the tendinous portion is longer and the muscular portion relatively shorter than in Storks and Herons, thus showing a degenerate condition. The rounded tendon underlying the biceps is more interesting. In birds where the curious muscle known as the ambiens is present, the tendon of that muscle passes through the knee-joint, passes under the biceps tendon, sometimes with an anchor to the edge of the fibula, and then forms a third head of origin of the perforated flexors,

precisely similar in position and relations to the rounded tendon under the biceps in *Baleniceps*. But for the fact that the tendon stops short at the head of the fibula and does not pass through the knee capsule to a normal ambiens muscle, it cannot be distinguished from the ambiens head of the perforated flexors. Garrod (17) first called attention to the interest of the ambiens muscle and regarded it as a major key to the classification of birds. He divided the Class into two Subclasses, the Anomalogonatae, containing the Piciformes, Passeriformes, and Cypseliformes in which the ambiens is never present, and the Homalogonatae, containing all the other groups of birds and showing that in them the ambiens was normally present. Among the Anomalogonatae there is no species in which the ambiens has been found; among the Homalogonatae there are families and genera in which it is absent, and Garrod believed that in such cases it had been secondarily lost. In a much later contribution to the subject (24), I showed that in the Night Heron and in *Eclectus*, birds without an ambiens but belonging to Garrod's Homalogonatae, there existed an ambiens head to the perforated flexors, absent in the Anomalogonatae, and plainly suggesting that it was a remnant of the ambiens muscle. In a memoir on the anatomy of the Hoatzin (27) I was able to describe from dissections of different examples of that bird, a case of this possible degeneration in actual progress. Garrod had dissected both legs in three examples of the bird and in all cases found the ambiens small but normal above the knees, but in five out of the six legs it was lost at the knee-joint. He does not appear to have had his attention called to the importance of the ambiens head of the perforated flexors. I examined each leg in two examples, and found in every case an ambiens head to the perforated flexors, but the ambiens muscle in some instances absent above the knee, in others small and lost at the knee-joint. It may therefore be taken as established that the ambiens head of the perforated flexors represents a vestige of a complete ambiens muscle, and its existence in *Baleniceps* is of morphological rather than systematic importance. The ambiens is usually present in the Steganopods, present in the Spoonbills, present in some genera of Storks absent in others, absent in *Scopus*, absent in Herons and *Baleniceps*, but in the last two cases its recent loss is shewn by the existence of the vestige to which I have now called attention.

Flexor profundus or *perforans* and *Flexor longus hallucis*.—The deep flexor as in Storks and Herons arises by fleshy digitations (text-fig. 129, Fl.Pro.) from the side of the fibula and from down the shaft of the tibia to form a strong round tendon. The flexor longus hallucis comes from the inner surface of the outer condyle of the femur (text-fig. 129, Fl.Hal.) and similarly forms a round tendon. The two tendons pass down to the flexor surface of the foot in the usual way. The deep flexor (text-fig. 131, B) breaks up into a branch for digits 2, 3, 4, and the hallucis tendon,

crossing over the profundus, runs to the hallux, but sends a long slender branch which joins the profundus tendon just before that divides for the digits. The condition corresponds with what Gadow (16, p. 195) calls type I. The hallucis tendon crosses over the profundus to reach the hallux, but sends a vinculum to it. In Storks and Herons the condition is essentially similar, but in the former group the vinculum is stronger and may be in separate slips; in *Scopus* and the Herons the vinculum is much more slender and may be absent. For comparison I figure the condition in a Stork (text-fig. 131, S), a Heron (text-fig. 131, A), and in *Balæniceps* (text-fig. 131, B).

Text-fig. 131.

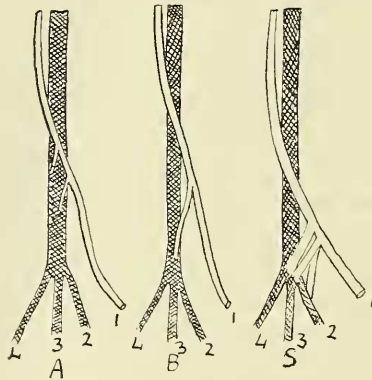


Diagram of Deep Flexor Tendons in A, *Nycticorax*; B, *Balæniceps*; S, *Leptoptilus*.

The *longus hallucis* tendon is in outline, the *flexor profundus* is shaded.

1. Hallux. 2, 3 & 4. 2nd, 3rd & 4th digits.

Popliteus.—There was only one of these little muscles stretching across between the head of the fibula and the tibia. In *Leptoptilus* I noted two.

SUMMARY OF MUSCULAR ANATOMY.

Garrod's hope, excited by his extraordinarily interesting pioneer work, that muscular anatomy would furnish a sure clue to the classification of birds has not been fulfilled. Garrod relied chiefly on the presence or absence of certain muscles which he found to vary from group to group. Gadow, who has attempted on a complete scale to apply to the system Garrod's group of muscles, using the additional facts made known by Beddard and other writers, appreciated that as these muscles were a common heritage of all birds, the presence of any of them in any group of birds could not be taken as a guide to the systematic position of that

group. He was disposed, however, to attach value to the loss of any of these muscles, and accordingly regarded the loss of this or that muscle as one of the characters to be employed in judging of the relationships of groups. Even this cautious use seems to me to be going too far. At present I do not know of any reason why we should suppose that a particular muscle may not have been lost independently many times; that is to say of any reason why a bird that has lost its femoro-caudal muscle should be more nearly related to another bird with a similar loss than to a bird which has retained the possession once common to all three. The loss is what I have described as a multiradial apocentricity. Possibly when we know as much of the development and morphology of the muscles used by Garrod, as Fürbringer has taught us in the case of the shoulder and wing muscles, we shall be able to make more definite use of muscular anatomy in systematic ornithology. As, however, muscular anatomy has been used freely, I may give a summary of the chief facts from which more confident anatomists would draw inferences.

Comparison of Herons, Storks, *Scopus* and *Baleniceps*.

Peculiar to *Baleniceps*.

Absence of latissimus dorsi metapatagialis. (? *Scopus*.)

Absence of humeral head of biceps brachii. (Unique.)

Absence of deltoides minor. (? *Scopus*.)

Absence of teres minor. (? *Scopus*.)

Origin of serratus superficialis posterior confined to dorsad of uncinatæ processes. (Same in *Phenicopterus*.)

Accessory origin from tip of scapula of serratus metapatagialis.

Common to *Baleniceps* and *Scopus*.

Condition of deltoides patagialis and patagial tendons.

Expansor secundariorum vestigial or absent (so also in most Steganopods).

Common to *Baleniceps* and Herons.

Presence of peroneus profundus.

Ambiens reduced to a distal vestige (said to be absent in *Scopus*, present in Storks).

Deep flexor tendons.

Common to *Baleniceps* and Storks.

Peculiar arrangement of tendon of insertion of latissimus dors. post.

Practical doubling of pectoralis major (also in some Steganopods).

Presence of post-acetabular portion of glutæus maximus (at least in some Storks; ? *Scopus*).

Oval origin of obdurator internus (also in most Steganopods).

Common to *Baleniceps*, *Scopus*, Herons, Storks and most Steganopods (but also in many other groups).

Absence of biceps slip to patagium.

Absence of accessory femoro-caudal.

Clearly, so far as the evidence from muscular anatomy goes, *Baleneiceps* is an ally of *Scopus*, Herons and Storks, and shares many characters with these birds and Steganopods. The two facts that impress me most are the close similarity of the rather highly specialized patagial muscle and tendons in the case of *Baleneiceps* and *Scopus*, and the very remarkable condition of the pectoralis thoracicus found in *Baleneiceps* and Storks, but which probably also exists in *Scopus*, and certainly in *Pelecanus* and some other Steganopods.

OSTEOLOGICAL NOTES.

As the osteology of *Baleneiceps* has been described at length in W. K. Parker's well-known monograph (33), and as I have not the time at my disposal to make the elaborate study of the different types of Storks and of Herons which is necessary before final conclusions can be drawn from the skeleton of *Baleneiceps*, I must content myself with a few notes on some of the salient points which struck me as requiring special study.

Occipital condyle.—In *Baleneiceps* this, seen from in front and below, has much the appearance of a moderately dolicocephalic human cranium. It is sessile, elongated antero-posteriorly, and its posterior margin, where it projects slightly into the *foramen magnum*, is convex. In the Herons the condyle is transversely elongated, and the posterior margin, where it projects into the *foramen magnum*, is the broadest part, is concave and slightly grooved, as if to form the beginning of two condyles. In *Scopus* the condyle is also transversely elongated but not so much as in Herons, and its foraminal margin is abruptly truncated. In *Anastomus*, *Dissura*, *Xenorhynchus*, and *Ciconia* the long axis is transverse, and the foraminal margin is concave or notched. In *Tantalus*, on the other hand, the condyle is nearly spherical, and although a notch may just be indicated, the foraminal margin is convex. The configuration of the condyle in *Baleneiceps* is, therefore, unlike *Scopus*, Storks or Herons, but it is most nearly approached by the *Tantalus* Storks.

Paroccipital processes.—The broad, thin and shell-like processes which bend down over the articulation of the quadrate are repeated on a smaller scale in *Tantalus*, where however the laminae are relatively thicker and less extensive. In other Storks they are replaced by similarly situated, thick and curving ridges. In *Scopus* and Herons all appearance of the shell-like arrangement is absent.

Basitemporal plate.—In *Baleneiceps* the anterior margin of this has a crescentic free edge which nearly meets at each side a curved lamina projecting from the basisphenoid, so that the Eustachian tubes are nearly floored in below. Parker wrote that "in the Heron these parts are essentially a miniature" of those in *Baleneiceps*, adding that this "is certainly not a faint and superficial mark of affinity." But the similarity extends to *Scopus* and

Storks. In Herons the anterior margin is slightly pointed, and in *Scopus* and the Storks, including *Tantalus*, it is rather more sharply pointed, but the general relations and particularly the relations to the laminae from the basisphenoid, which I shall now describe, are more like those of *Baleniceps* in the case of Storks than of Herons.

Basisphenoid.—Seen from below this has the usual "T-shaped" appearance, the cross bar of the "T" being contiguous with the anterior edge of the basitemporal, the main limb forming the rostrum. In *Baleniceps* delicate crescentic lamellae project backwards nearly meeting the front edge of the basitemporal plate and with it forming a floor for the Eustachian tubes. The condition of these laminae in *Tantalus* most closely resembles that of *Baleniceps*; in the other Storks the laminae are less complete, and they are least complete in the Herons and *Scopus*. The rostrum from the "T" cross bar to the attachment of the pterygoids is a stout, broad beam of nearly equal width throughout its length in *Baleniceps*. The other birds in the set I am considering present a series ranging from *Baleniceps* through *Tantalus*, the typical Storks, and *Scopus*, to the Herons which present the end of the series most remote from *Baleniceps*. The rostrum gradually in the series changes from an even beam to a sharply contracting, almost triangular outline, and its smooth ventral curved surface becomes first slightly ridged, and then strongly carinate as in Herons.

Orbital septum.—This is completely ossified in *Baleniceps*, *Scopus*, all the Storks, including *Tantalus*; very incomplete in the Herons, including *Canceroma*.

Lacrymal.—As Parker has described, the lacrymal of *Baleniceps* is highly peculiar, although no doubt the peculiarity is partly adaptive in relation to the enormous beak. It is a stout vertical strut forming the anterior wall of the orbit, firmly ankylosed below with the jugal and maxilla, and above with the nasal. On the roof of the skull it forms the external portion of the fronto-maxillary hinge which runs as a transverse suture across the forehead, being thus entirely anterior to the hinge. A thin vertical lamina projects from it into the cavity of the orbit, which is pierced by a large lacrymal foramen, external to the nasal cavity. In *Scopus* the lacrymal is a vertical beam scooped out on its orbital face for the lacrymal canal, but hanging down freely along the front of the orbital cavity, until it almost meets but does not actually touch the jugal. It has no contact with the maxilla and depends from the orbital edge of the frontal, behind the fronto-maxillary hinge, and with no more than the minutest overlap to the nasal on the distal aspect of the hinge. In Storks of the genus *Tantalus* the lacrymal is suspended from the orbital edge of the frontal behind the hinge, with just a trace of overlap across it to the nasal. From this point of suspension the flat external face hangs vertically downwards, gradually narrowing, and free from the maxilla and not reaching

the jugal below; it has a stout lamina projecting into the orbital cavity transversely to the long axis of the skull and pierced for the lacrymal canal. In the typical Storks and in *Anastomus*, the external face of the lacrymal is roughly triangular, the convex basal line being attached to the orbital edge of the frontal, but definitely extending forwards across the hinge to form a very loose connection with the nasal, not more than a fifth of the whole dorsal edge of the bone. From this, the rapidly narrowing triangle hangs down in front of the orbit and is far from reaching the jugal and has no connection with the maxilla. The inwardly projecting flange is a very thick beam pierced for the lacrymal canal. In the Herons, the relations are a still further exaggeration of the difference between Storks and *Balænicæps*. The outer surface of the lacrymal is triangular with a very broad base of attachment to the frontal behind the hinge, a small loose overlap to the nasal in front of the hinge, and with no connection with jugal or maxilla. The inwardly directed flange is absent and there is no lacrymal canal.

In the case of the lacrymal bone, therefore, *Balænicæps* and *Ardea* stand at opposite ends of a series, *Tantalus* being nearest to *Balænicæps*.

Nasal region.—The nostrils in *Balænicæps* are impervious, a stout nasal septum being developed. Gadow states that they are pervious in *Scopus*, but this is a mistake; a very thin lamina of bone very slightly fenestrated separates them. In all the Herons and Storks they are pervious, the cavity from one nostril to the other being large and quite open. The skull is holorhinal as in *Scopus*, *Ardea*, *Cancroma* and all the Storks including *Tantalus*, but in many, especially the larger Storks, the proximal end of the nasal bone shows a line of weakness running up towards the naso-frontal hinge and leading to the schizorhiny seen in *Ibis*. From the anterior border of the nostril a groove runs along the surface of the beak to the extreme anterior end, only the hook of the beak projecting beyond it. Beddard appears to lay some stress (4, p. 434) on this point because he says that the groove is "precisely like that of *Scopus* and *Cancroma*." It is like that of *Scopus*, but in *Cancroma* the groove is much wider and more shallow and does not reach the extreme anterior end. It is much more exactly repeated in the Pelican, the Ibis and the Flamingo. In *Ardea* it is represented by a groove which runs about half-way from the nostril to the anterior end of the beak; and in most of the Storks it is represented by a line of weakness in the bone reaching about half-way to the tip of the beak. This is specially well marked in *Tantalus*.

The nasal processes of the premaxillæ are so firmly fused with the adjacent nasals that their exact outline cannot be seen. It is clear, however, that they do not invade the frontal region but terminate distad of the fronto-maxillary hinge. This also is the case in *Cancroma* and Storks, including *Tantalus*, but in *Ardea*

and *Scopus* the nasals break the transverse line of the lunge, fitting into the frontals.

The anterior tip of the premaxilla is produced in *Baleniceps* to form the strong down-turned hook of the bill. *Scopus* repeats this on a smaller scale; in *Cancroma* the sharp point is not bent into a hook. In the other Herons and in Storks it is straight.

Palate.—The palate is desmognathous in *Baleniceps*, the maxillo-palatines being fused in the middle line, and the vomer represented by a triangular, very thin, ossification, the knife-like base of which divides the internal nares when seen from below. The condition in *Scopus* is almost identical, but at its proximal end, where it touches the central laminae of the palatine, the rather larger vomer shows a broader edge with the faintest suspicion of doubling. In the Storks, the vomer is relatively smaller even than in *Baleniceps* and there is no trace of forking. In *Cancroma* and *Ardea* the vomer is relatively very much larger and its edge is quite distinctly cleft between the palatines, each blade being attached to the palatine lamina contiguous with it. In this respect *Baleniceps* and the Herons are at the opposite ends of the series. With regard to the palatines, the most striking feature in *Baleniceps*, fully described by Parker, is the coalescence of the internal laminae to form a strong keel stretching back from the posterior nares to the pterygoid articulations. Allowing for differences in shape and proportion, the similarity with *Scopus* is close. The median keel is still more strongly marked in the Pelican and in *Plotus*; it is represented in Storks by a delicate median ridge, but in *Cancroma* and *Ardea* the internal laminae of the palatines remain completely separate.

Pterygoids.—I notice no significant differences between the pterygoids of *Baleniceps* and those of *Scopus*, Storks and Herons. Basipterygoid articular processes are absent in all, and I have not found even any rudimentary trace such as is common in the Pelican. The ventral distal end of each pterygoid is smoothly rounded in *Baleniceps* and *Ardea*; in *Cancroma*, *Scopus* and most of the Storks it shows a sharp keel running out as if to meet the outer lamina of the palatal.

Quadrate.—This is substantially alike in *Baleniceps*, *Scopus*, Herons and Storks, but the orbital process in *Baleniceps* is almost triangular, the blunted apex projecting into the orbital cavity. In *Scopus* the orbital process is rather blunter; in *Tantalus* more acute, but in Storks generally it tends to expand to a spatulate end, and in the Herons, including *Cancroma*, the apex is much expanded.

Quadratjugal bar.—This is enormously stout in *Baleniceps*, and the separate portions of which it is composed cannot be distinguished. In all the other birds I am considering, it forms a slender, much elongated rod.

Temporal cavity.—The boundaries of the temporal cavity present interesting modifications in *Baleniceps* and its allies.

Unfortunately, owing to the very complete union of the bones concerned, these cannot be interpreted completely without the examination of very young skulls, but comparison of adult skulls shows a good deal worth noting. In *Balaniceps* the size of the brain is small in proportion to the size of the bird, with the result that the skull is very short between the orbit and the posterior end. Attachment for the powerful temporal muscle is increased by the strength and size of the postfrontal process (Pl. LXXXI. fig. 1), which depends as a triangle of bone behind the orbit, with the external face strongly ridged. The blunted apex of the triangle reaches nearly half-way down to the quadrato-jugal bar and is continued to a strong tubercle on the latter by a fibrous band. The central portion of the band has a separate ossification, and it would not be surprising to find, in an old bird, that calcification of the fibrous band had joined this central ossification with the postfrontal above and the jugal below, to form a complete beam of bone separating the orbital and temporal cavities externally. Owing to the complete fusion of the bones, it is impossible to be certain as to the exact composition of the postfrontal. A more primitive skull like that of *Dromæus* (in which the proportion of the temporal region to the rest of the skull closely resembles that in *Balaniceps*) shows that the alisphenoid contributes the main portion of the postfrontal, and that the frontal grows down over it only about half-way. In *Balaniceps* it appears as if the frontal covered the alisphenoid right down to the lower end of the postfrontal, and on the posterior face the alisphenoid may itself be covered by a process of the squamosal. On the other side of the temporal cavity in many birds the squamosal sends forwards and downwards from just over the quadrate articulation a stout beam of bone projecting towards the point of the postfrontal. In *Balaniceps* this is represented only by a narrow edge projecting over the quadrate articulation. *Scopus* (Pl. LXXXI. fig. 2) has like *Balaniceps* also a small brain and narrow temporal space. The postfrontal has almost exactly the relations of that of *Balaniceps*, but it does not reach nearly so far towards the jugal. The spur of the squamosal is minute, and allowing for differences in the strength of the muscular attachments, this region is almost the same in *Scopus* and *Balaniceps*.

In a large Stork like *Xenorhynchus* (Pl. LXXXI. fig. 3) there is an arrangement strikingly different in appearance but which, none the less, can be interpreted easily. The brain is still small and the temporal cavity narrow. The postfrontal triangle narrows very rapidly and is continued downwards as a slender bar which stops short long before the jugal is reached. Close scrutiny seems to show that the frontal contributes a superficial splint-like factor, running down almost to the tip on the anterior face, and that the squamosal forms the greater portion of the lower and posterior part, but how much the alisphenoid contributes it is impossible to say. The spur of the squamosal from over the

quadrate articulation is enormous and forms a powerful process which runs downwards and forwards to meet and fuse with the tip of the postfrontal. In a smaller skull, like that of the *Dissura* (Pl. LXXXII. fig. 1), the arrangement is practically identical, but the postfrontal, although it meets the squamosal spur, is much more slender, and the frontal factor does not appear to reach more than half-way down.

In *Tantalus* (Pl. LXXXII. fig. 2) the brain is relatively slightly longer and larger. The squamosal spur is exactly as in *Xenorhynchus* and *Dissura*, but two things have happened to the postfrontal. In the first place it is much shorter, and does not reach the squamosal spur. In the second place the triangular base is very much wider and is deeply notched in front, with the result that it has an anterior and smaller portion corresponding exactly to the anterior margin in all the other birds I have been describing here, but certainly with no squamosal factor, and a longer portion running down towards the point of the squamosal spur, corresponding with the posterior part of the postfrontal in other birds and certainly consisting chiefly of alisphenoid and squamosal factors.

The condition in *Cancroma* (Pl. LXXXII. fig. 3) can now be followed easily. The brain is still larger relatively; the squamosal spur is reduced, and the separation between the two parts of the postfrontal, only just apparent in *Tantalus*, is well marked. The purely frontal, anterior portion is the stouter of the two. In *Ardea* (Pl. LXXXIII. fig. 1), where again the brain is still larger, the squamosal spur is relatively rather small, but the separation between the two parts of the postfrontal is very wide indeed.

As this matter appears to be of some interest, and as I have not found it discussed, I shall continue the description outside the immediate relatives of *Baleniceps*. The Pelican (Pl. LXXXIII. fig. 2) shows a further extension of the series. The squamosal spur is as in *Ardea*, but the two portions of the post-frontal are even further separated, and the posterior of the two is reduced to a mere tubercle, intermediate in position between the squamosal spur and what would normally be taken to be the postfrontal. In *Plotus* (Pl. LXXXIII. fig. 3), which has a very large brain indeed, the squamosal spur is small, there is a mere stump to represent the posterior portion of the postorbital process and this is actually nearer the squamosal spur than it is to the anterior representative of the postfrontal.

I do not suggest that the series, as I have arranged it, is phylogenetic, but it is a striking example of the differences that identical morphological material may exhibit in allied birds, and a warning against the hasty drawing of conclusions as to systematic position from the comparison of one or two presumably allied birds. So far as this point goes, *Baleniceps* and *Scopus* stand together as birds with small brains, with the squamosal spur slight and the postfrontal process simple. Storks form a

second group also with small brains, with the squamosal spur very highly developed, frequently reaching the postfrontal, and with the latter simple, but in *Tantalus* showing the beginning of cleavage. *Cancroma* and the other Herons form a third group, characterized by larger brains, with the squamosal spur reduced as in the first group but with the postfrontal split into two separate processes of which the anterior tends to become the more important.

Mandible.—The fusion of the component parts is so complete that I could not see any trace of sutures. The most notable feature is the absence of the projecting spur of the angle, an absence which *Balæniceps* shares with *Scopus*, all the Storks and *Cancroma*, in all of which the end of the mandible behind the articular cavities for the quadrate is as if abruptly sawn off, while in *Ardea* and typical Herons it is produced backwards as a long rounded spur.

Vertebral column.—As Parker (33) and Gadow (16, p. 76) have pointed out, there are 17 cervical vertebræ in *Balæniceps*, 16 in *Scopus*, 17 or 18 in Storks, and 18 to 20 in Herons. The carotid canal is complete in all this group of birds. The individual vertebræ are very much shorter antero-posteriorly in *Balæniceps* than in the Herons and *Scopus*; the Storks are intermediate between *Balæniceps* and Herons in this respect, which no doubt is purely adaptive, but it suggests at least that *Balæniceps* is not very closely related with Herons. Parker states that there are no foramina for the vertebral arteries on the sides of the atlas in *Balæniceps* and in its allies. They are certainly absent in *Balæniceps*, but present, although small and limited to the anterior lateral part of the atlas, in *Ardea*, *Cancroma* and *Scopus*, and present and large in Storks.

The thoracic vertebræ have no hæmapophyses in *Balæniceps*, *Cancroma*, *Ardea* and *Xenorhynchus*, but there is a very small unpaired process in *Tantalus*.

Sternum.—The posterior lateral processes are very long in *Balæniceps*, projecting well behind the metasternum; in *Scopus*, Herons and Storks, they are short, not projecting behind the metasternum. The notch separating the posterior lateral process from the metasternum is rounded in *Balæniceps*, *Scopus* and Storks, angular in *Ardea* and *Cancroma*. Parker figured a small posterior intermediate process, and compared it with that of the Ibis, but it was completely absent in the skeleton I examined, as well as in Herons, Storks and *Scopus*.

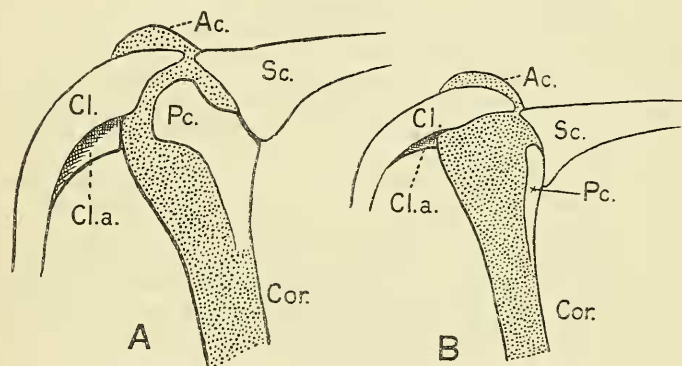
The internal spine of the sternum is absent in *Balæniceps* as in *Scopus*, Storks and Herons, but the external spine is also absent in *Balæniceps*, small in *Scopus*, small or absent in Storks (best developed in *Tantalus*), large and prominent in Herons including *Cancroma*.

Furcula.—In *Balæniceps* the clavicles are joined to form a very short-stemmed "Y," the stem of the Y as well as the distal ends of the diverging arms being strongly anchylosed to the

projecting anterior end of the keel of the sternum. There is no trace of a median process opposite the hypocleideum between the arms of the furcula. Anchylosis with the keel may be regarded as an adaptive character. It is as complete in the Pelican as in *Baleniceps*: it exists in some of the large Storks, but in Storks and Herons generally the connection is by ligament. In *Scopus* the furcula is far short of reaching the keel. In *Scopus*, Storks and Herons including *Cancroma*, the furcula is more "U"-shaped; the median forward process between the arms of the "U" is absent in *Scopus* and Storks as in *Baleniceps*, but is well-marked in Herons.

The proximal end of each clavicle where it reaches the coracoid has a very strong flange (text-fig. 132, A, *Cl.a.*) which articulates

Text-fig. 132.

Shoulder-girdle Articulation in *Baleniceps* and *Scopus*.A. *Baleniceps*. B. *Scopus*.

- Ac. Acrocoracoid process of Coracoid.
- Cor. Coracoid.
- Pc. Procoracoid process of Coracoid.
- Cl. Clavicle.
- Cl.a. Acrocoracoid process of Clavicle.
- Sc. Scapula.

directly with the anterior border of the coracoid. A similar flange is present in *Scopus* (text-fig. 132, B, *Cl.a.*), and in its place there is a minute flat articular facet in *Tantalus*, but it is absent in Storks generally and in Herons including *Cancroma*, the clavicle being attached to the acrocoracoid only by strong ligaments. The development of this flange in *Baleniceps* is a very strongly marked character, but too much weight cannot be laid on this similarity with *Scopus*, for the acrocoracoid flange of the clavicle is equally well marked in the Pelican, in *Plotus*, in Cormorants and Gannets, and in Birds-of-Prey.